

Review of the Genus *Megalomma* (Polychaeta: Sabellidae) in Australia with Description of Three New Species, New Records and Notes on Certain Features with Phylogenetic Implications

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ABSTRACT. The aim of this paper is to document the presence, diversity and distribution of *Megalomma* in Australia. This could be considered the first valid record of the genus in this continent as the only species previously recorded was transferred to another genus (Knight-Jones, 1997). The species diversity found during this study indicates that the occurrence of *Megalomma* in Australia has been overlooked, as the genus is well represented with at least seven species, living in a range of habitats and depths, and three of which are herein described as new, *M. phyllisae* n.sp., *M. inflata* n.sp. and *M. interrupta* n.sp. Cladistic analyses have been performed after the generation of a matrix of morphological features including those of some well documented species, in order to find informative characters for grouping species and to test the validity of previous artificial classifications. According to the phylogenetic hypothesis presented herein, the fusion of dorsal collar margins to the faecal groove and the presence of collar “pockets” characterizes the apomorphic clade of *Megalomma* species but the number of radiolar eyes is a homoplastic character, varying substantially in the *Megalomma* radiation, meaning that the traditional groups should be reviewed. A dichotomous key is provided to facilitate Australian species identification.

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The genus *Megalomma* Johansson, 1925 is characterized by the presence of subdistal, unpaired, sessile, compound eyes with distinct ommatidia in at least dorsal-most radioles, a unique feature among sabellid polychaetes (Fitzhugh, 1989; Fitzhugh & Rouse, 1999), but to date no phylogenetic analysis of the genus has been performed for assessing the relationships among the species.

The number of species included in this genus has increased in the last decade especially after detailed taxonomic studies in Thailand (Nishi, 1998; Fitzhugh, 2002), the Grand Caribbean (Tovar-Hernández & Salazar-

Vallejo, 2006; Giangrande *et al.*, 2007), the Eastern Tropical Pacific (Tovar-Hernández & Salazar-Vallejo, 2008) and the Mediterranean Sea (Giangrande & Licciano, 2008), bringing the number of species to 31 (see Table 2).

Most of the taxonomic accounts are based primarily on three morphological characters proposed by Knight-Jones (1997): fusion of dorsal collar margins with the faecal groove, presence of collar “pockets” and distribution of subdistal radiolar eyes. Based on the combination of these characters she produced a table of species’ groups that has been used by subsequent authors (e.g., Nishi, 1998;

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Fitzhugh, 2003; Tovar-Hernández & Salazar-Vallejo, 2006, 2008). However, these Groups have not yet been tested for evolutionary meaning and therefore should be treated as operational only.

Some features that have been traditionally included in the description of species and used to characterize the abovementioned Groups (Knight-Jones, 1997) are difficult to interpret and/or to classify into discrete character states. The most obvious case is the form and development of the dorsal margins of collar. In some species, a low membrane or ridge appears to be a continuation of the dorsal collar margin, making difficult the interpretation of whether or not the collar is fused into the faecal groove, and therefore also whether pockets are present or absent. See for example the discussion about placement of *M. neapolitanum* (Claparède, 1868) into either Knight-Jones' Group 2A or 1A (Giangrande & Licciano, 2008). Some other species with the dorsal collar margins fused to the faecal groove (Group 1A and 1B in Knight-Jones' categories), show an enlargement of the collar on its dorsal margins forming dorsal lappets or flaps on both sides of the faecal groove. This is the case for *M. acrophthalmos* (Grube, 1878), *M. fauchaldi* Giangrande *et al.*, 2007 and *M. vesiculosum* (Montagu, 1815) (Knight-Jones, 1997; Giangrande *et al.*, 2007). But other similar species with these well-developed collar dorsal lappets such as *M. mushaense* (Gravier, 1908) and *M. nechamae* (Knight-Jones, 1997) were considered to have the collar not fused to the faecal groove, and these lappets were interpreted as a development of the dorsum or peristomium and not of the collar (Knight-Jones, 1997).

It has also been observed that some of these "diagnostic features" can be misinterpreted when the number of specimens examined is small, as some species show variation in the number and development of subdistal compound eyes (Fitzhugh, 2003) which may not necessarily be related to size of the specimens (Nishi, 1998).

A worldwide review of the genus is currently being undertaken (Tovar-Hernández pers. comm.) in which the groups proposed by Knight-Jones (1997) will hopefully be reassessed.

Nine species of *Megalomma* have been reported from the Indo-Pacific: *M. acrophthalmos* from Philippines, *M. miyukiae* Nishi, 1998 and *M. multioculatum* Fitzhugh, 2002 from Thailand, *M. pacificum* Johansson, 1927 from Gilbert Islands, *M. suspiciens* (Ehlers, 1904) and *M. kaikourense* Knight-Jones, 1997 from New Zealand, *M. trioculatum* Reish, 1968 from Marshall Islands, and *M. cinctum* Fitzhugh, 2003 from Taiwan. Only one species, *M. vesiculosum*, was reported from Australian coasts, in an Australian polychaetes interactive key (Wilson *et al.*, 2003). However, no material identified as such has been found in any Australian museum collections, leading to the conclusion that this was a mistake (Wilson, pers. comm.). The only

other recorded presence of *Megalomma* in Australia, was *Megalomma monophthalma* from Queensland by Augener in 1922, as *Sabella monophthalma* Augener, 1922, but this species has subsequently been synonymized with *Stylomma palmatum* (de Quatrefages, 1866) by Knight-Jones (1997). Therefore, the present paper is the first valid record of the genus in Australia.

One of the aims of this study is to document the presence of *Megalomma*, its diversity along the Australian coastline and to record the species' distribution. Some features traditionally used to separate species into groups as well as others proposed herein, have been tested for potential value for taxonomic and systematic accounts.

Materials and methods

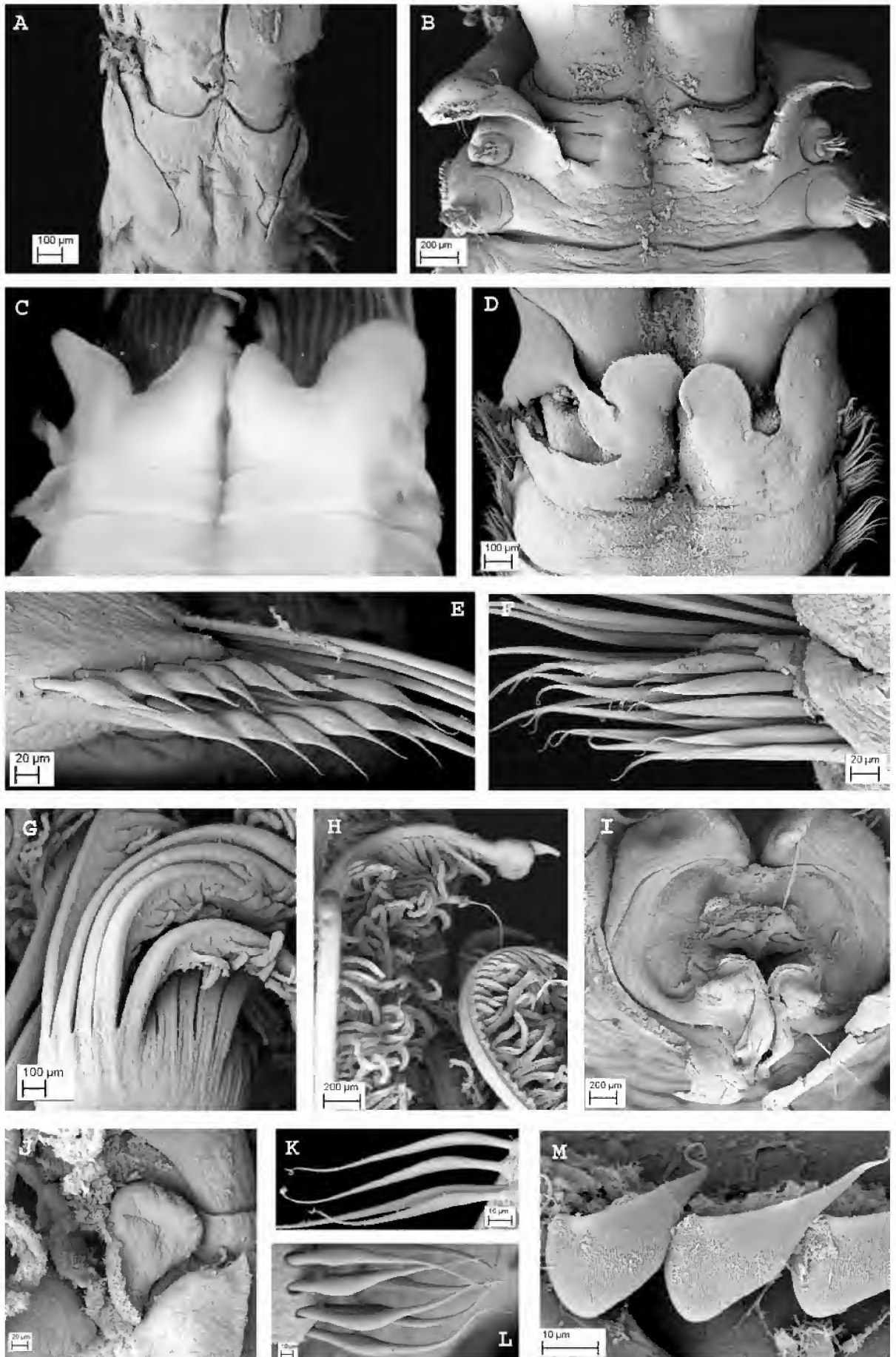
Material examined. Specimens from Australian coasts were studied from collections housed in the Australian Museum (AM), Sydney; Museum and Art Gallery of the Northern Territory (MAGNT), Darwin, and Museum Victoria (MV), Melbourne. This included material collected in several surveys and projects around the Australian coast. Some specimens were also collected for live examination and then fixed in 10% seawater formalin and preserved in 80% ethanol or in 95% ethanol for further molecular studies. Other specimens belonging to other collections were also studied for comparison: Zoologisches Museum Hamburg, Germany (ZMUH) and Smithsonian Institution, National Museum of Natural History, United States of America (USNM).

Some parapodia (usually from first and seventh thoracic chaetigers and some from the abdominal region) were removed and mounted on slides to examine chaetae. The internal structure of the radioles were examined by cutting thin transverse sections of these structures at base level and mid-length with a surgical blade and mounting them on slides. Line drawings were made to scale with a drawing tube attached to either a stereo or compound microscope. Some specimens were dehydrated in ethanol, critical point dried and covered with 20 nm of gold and examined under a Zeiss Evo LS15 scanning electron microscopy, using Robinson backscattered and ET secondary electron detectors.

Cladistic analysis

Taxa considered for the analyses. A total of 20 species of *Megalomma* were included as the ingroup, including the type species, two species of each of the groups proposed by Knight-Jones (1997) and used in subsequent studies (e.g., Nishi, 1998; Fitzhugh, 2003; Tovar-Hernández & Salazar-Vallejo, 2008), as well as all the Australian species described herein. The data were obtained from direct study of specimens, when these were available, and descriptions in the literature. *Demonax leucaspis* Kinberg 1867, was

Figure 1 (facing). SEM. (A–D) Types of collar dorsal margins: (A) separated and with no pockets as in *Megalomma* sp. 2; (B) fused to the faecal groove and forming vestigial pockets on each side, as in *Megalomma interrupta* n.sp.; (C) fused to the faecal groove and with short dorsal lappets as in *M. phyllisae* n.sp.; (D) fused to the faecal groove and with spatulate dorsal lappets as in *M. cf. acrophthalmos*. (E,F) Types of inferior thoracic chaetae: (E) *Megalomma phyllisae* n.sp. with broadly hooded chaetae type A and (F) *M. cf. acrophthalmos* with broadly hooded chaetae type B. (G,H) Shape of radioles: (G) *M. cf. acrophthalmos* with quadrangular external margins at the base; (H) *M. inflata* n.sp. with quadrangular distal margins of radioles. (I,J) Parallel lamellae and ventral sacs, smaller in (I) *Megalomma* cf. *miyukiae* and, more developed in (J) *M. interrupta* n.sp. (K,L) Abdominal chaetae: (K) narrowly hooded and (L) broadly hooded. (M) Companion chaetae of *M. cf. miyukiae* showing the asymmetrical and dentate membrane.



selected as the outgroup, as this genus has been considered to be the sistergroup of *Megalomma* in previous phylogenetic analyses (Fitzhugh, 1989, 2003; Fitzhugh & Rouse, 1999).

Characters and states. The characters and their states used for analysis were those considered as diagnostic in traditional taxonomic studies (Perkins, 1984; Knight-Jones, 1997; Fitzhugh, 2002, 2003; Giangrande *et al.*, 2007; Giangrande & Licciano, 2008; Tovar-Hernández & Salazar-Vallejo, 2008), as well as others observed to vary within *Megalomma* species by us and other workers (Tovar-Hernández & Salazar-Vallejo, 2008; Fitzhugh, 2003; pers. obs.). Absence/presence and multistate coding methods were used; multistate characters were equally weighted and unordered. Missing data were scored with “?”, inapplicable data with a hyphen. The score given for each state implies nothing about polarity or order.

The material studied for the present study included the whole range of variability of development of the dorsal collar margins described so far in *Megalomma*. *Megalomma* sp. 2 displays collar margins that are separated by a wide gap and therefore has no dorsolateral pockets (which are pouch-like structures formed by the collar and peristomium) (Fig. 1A); *Megalomma interrupta* n.sp. has collar margins that are not fused to the faecal groove but low pockets are present (Fig. 1B); *Megalomma phyllisae* n.sp. has collar margins fused to the faecal groove, pockets present and low dorsal lappets (Fig. 1C); and *M. cf. acrophthalmos* has dorsal lappets that are well developed and spatulate-shaped (Fig. 1D).

In specimens that display only shallow membranous dorsal collar margins that extend all the way to the faecal groove (and also form shallow pockets dorsolaterally), the interpretation of these structures was based on whether we could insert forceps under the margin and the tip was hidden by the margin, indicating that there was a membranous extension of the collar across to the faecal groove (Fig. 1B), or not (Fig. 1A). Where dorsal lappets are present, this is not ambiguous, as these are extensions of the collar and hence the collar is obviously fused with the faecal groove (Fig. 1C,D).

After examination of several species of *Megalomma*, we have observed two general forms of inferior thoracic chaetae. They all match the category of “broadly hooded” chaetae as figured by Perkins (1984) and Fitzhugh (1989), and also referred to as “subspatulate” by other workers. They have a short distal hood, gently curved margins and a fine, elongate tip (Fitzhugh, 1989). Under light microscopy the hood can be distinguished on both sides of the shaft as symmetrical wings (different to a narrowly hooded chaetae where the hood is only visible on one side) and the shaft almost reaches to the tip of the chaetal hood (different to “paleate” chaetae which have short emergent shafts). The *Megalomma* species described in this paper display two kinds of “broadly hooded” inferior thoracic chaetae: those with the distal end narrowing abruptly and which are referred to from now on in the text as type A (Fig. 1E), and those with a progressively tapering distal tip, referred in the text as type B (Fig. 1F).

Analytical methods. A matrix including 20 terminal taxa and 14 characters was constructed in NDE, Nexus Data Editor (Page, 1998). The parsimony analysis was performed using NONA 2.0 (Goloboff, 1993). Tree searches were complete using the heuristic search, with the multiple tree bisection and reconnection (TBR + TBR) strategy, selecting

25000 replicates and holding 5000 trees at each step and starting 5 trees per replicate. Cladogram topologies and character-state optimization were examined using Winclada (Nixon, 2002), showing only unambiguous changes. Nodal supports were determined calculating jackknife proportions from 1000 replicates using TRB, in Winclada. Tree metrics are abbreviated as follows: tree length (TL), consistency index (CI), and retention index (RI).

List of characters and states used:

- 1 Subdistal sessile compound eyes: (0) absent; (1) present.
 - 2 Arrangement of subdistal eyes: (0) in dorsalmost pair radioles (one to 3 pairs); (1) in all radioles; (2) in most radioles; (3) in dorsal most and lateral.
 - 3 Rows of cells in radiolar skeleton: (0) four; (1) eight to ten; (2) more than 10.
 - 4 “Caruncle”: (0) absent; (1) present
 - 5 Ventral sacs: (0) absent; (1) present.
 - 6 Dorsal collar margins: (0) fused to faecal groove; (1) not fused to the faecal groove.
 - 7 Dorsal collar pockets: (0) absent; (1) present.
 - 8 Dorsal collar lappets: (0) absent; (1) present.
 - 9 Thoracic ventral shields: (0) separated from tori; (1) only shields in anterior segments in contact with tori; (2) all ventral shields in contact with tori.
 - 10 “Interramal eyespots”: (0) absent; (1) present.
 - 11 Inferior thoracic chaetae: (0) with the distal end narrowing abruptly (type A); (1) or with a progressively tapering distal tip (type B).
 - 12 Handle of thoracic uncini: (0) shorter than length of distance of main fang to breast; (1) 1–2 times length of distance from main fang to breast; (2) >2 times length of distance from main fang to breast.
 - 13 Companion chaetae: (0) with distal end inflated, dentate and with a tapering membrane (1) with an asymmetrical, teardrop-shaped membranous hood
 - 14 Abdominal chaetae: (0) narrowly hooded; (1) elongate, broadly hooded.
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The matrix of species, characters and states is presented in Table 3.

Taxonomic account

Megalomma Johansson, 1925

Type species. *Branchiomma kollikeri* Claparède, 1869, a junior synonym of *Amphitrite vesiculosum* Montagu, 1815 (see Tovar-Hernández & Salazar-Vallejo, 2008).

Synapomorphy. Presence of subdistal, sessile and compound radiolar eyes, at least on the internal margin of the dorsalmost pair of radioles (Fitzhugh, 1989).

Remarks. There are other morphological characters that have been included in the diagnosis of the genus (see last emendation by Tovar-Hernández & Salazar-Vallejo, 2008) and are herein assessed.

Megalomma has been attributed with rounded external margins of radioles, but some of the species described in the present study clearly show distinct externally quadrangular

margins along some length of their radioles (Fig. 1G). However, it is not easy to distinguish between the two states (see also Fitzhugh, 1989, p. 21), and this may not be a significant character anyway. The species studied have longitudinal bands of cilia on the outer lateral edges (Fig. 1H) as stated by Perkins (1984) but this feature is not unique to *Megalomma* and they have been described in other genera [e.g., *Laonome* (Capa, 2007)].

The radioles are supported by rows of vacuolated cells (referred to as the radiolar skeleton). The number of rows is variable within the genus and also within some of the species. It has been stated by Tovar-Hernández & Salazar-Vallejo (2008) that the maximum number of rows is 16, but some of the specimens described in this study (e.g., *M. phyllisae* n.sp., Fig. 4A) exhibit up to 30 cells in transverse section (see variability of rows in radiolar skeleton in Fig. 5).

In *Megalomma*, the ventral lips terminate ventrally in parallel lamellae, as defined by Nicol (1931) and Fitzhugh (1989), seen between the ventral lappets of the peristomial collar, and some species also possess vesicles “formed by the outpocketing of the parallel lamellae” called ventral sacs (as in Fitzhugh, 1989) (Fig. 1I,J).

Tovar-Hernández & Salazar-Vallejo (2008) described for the first time the existence of a caruncle in some *Megalomma* species, as an erect, triangular ciliated lobe, between the dorsal lips. The examination of Australian specimens has determined the presence of a smooth “keel” in some species but its detailed morphology, ultrastructure or function has not been studied. It does not appear to be homologous to the caruncle, rather it is a smooth projection of the peristomium arising between the dorsal lips, forming a ventrally-directed ridge.

Characters and states relating to chaetae and uncini should also be reconsidered, as there is probably more variation in the genus than has been recorded so far. Previous studies agree that notochaetae of the first chaetiger are elongate and narrowly hooded, as are the rest of the superior thoracic chaetae (Perkins, 1984; Fitzhugh, 1989, 2003; Tovar-Hernández & Salazar-Vallejo, 2008), and that the inferior thoracic notochaetae are broadly hooded (Perkins, 1984; Fitzhugh, 1989, 2003; Tovar-Hernández & Salazar-Vallejo, 2008) but with hoods variable in length (Tovar-Hernández & Salazar-Vallejo, 2008). Abdominal neurochaetae have been described as elongated, narrowly hooded chaetae (Perkins, 1984; Fitzhugh, 1989, 2003; Tovar-Hernández & Salazar-Vallejo, 2008) (Fig. 1K) but they could be interpreted as broadly hooded (but with long tips) in some species (Fig. 1L). The length of the thoracic uncini handle could also be considered as useful for discriminating between species as this varies from medium length (same length as the distance from main fang to breast) to long (twice the length of the distance from main fang to breast).

The thoracic companion chaetae possess a proximal shaft or handle, generally similar in length to the thoracic uncini handle, and a distal membrane that has been described as teardrop-shaped by most authors (Perkins, 1984; Fitzhugh, 1989, 2002, 2003), or as roughly symmetrical (Fitzhugh, 1989; Tovar-Hernández & Salazar-Vallejo, 2006; Giangrande *et al.*, 2007), or as asymmetrical (Knight-Jones, 1997). After studying the position of the small rows of teeth and the orientation of the tip of the distal membrane, we have concluded that the membrane is asymmetrical (Fig. 1M). There is some variation in the form of the companion chaetae

among different species, so this character may be useful from a systematic point of view.

Note: generic diagnostic characters have been omitted from species descriptions, In Table 2, we have incorporated the new species into Knight-Jones’ operational “Groups”, and we have re-interpreted collar fusion, lappets and presence of pockets for some taxa.

Megalomma phyllisae n.sp.

Figs 2A–E, 3, 4A,B, 5A

Material examined. **Victoria.** HOLOTYPE AM W13643, off Townsend Point, Corner Inlet, 38°48'S 146°33'E, 16 Dec. 1976, 1.5 m. PARATYPES AM W35476 (2 spec., fragment from incomplete spec. on SEM stubs AM M082 and M083), same locality.

Additional material. *Megalomma suspiciens* (Ehlers, 1904) ZMUH PE 1304, syntypes (4 spec.), French Pass, New Zealand, 1 m, 1897. *Megalomma trioculatum* Reish, 1968 USNM 38409, paratypes (2), lagoon side of Engebi Island, Eniwetok Atoll, Marshal Islands, 7 Sep. 1956.

Diagnosis. Species characterized by a combination of the following features: subdistal compound eyes in all except ventralmost radioles, radiolar skeleton with more than 25 cells in transverse section, dorsal margins of collar fused to faecal groove forming flanking pockets on each side, caruncle absent, and inferior thoracic chaetae with progressively tapering distal tip (type B).

Description. Holotype 135 mm long, 5 mm wide; with eight thoracic and 107 abdominal chaetigers. Crown slightly longer than thorax, 15 mm long, with 30 radioles on left side and 28 on right side arranged in two semicircles. External margin of radioles quadrangular (Fig. 2A,B). Tip of radioles shorter than pinnules (Fig. 2B). Radiolar skeleton composed of more than 25 cells in transverse section (Fig. 5A). All radioles except for last two pairs of ventral radioles with a subdistal compound eye, eyes diminishing in size to ventral radioles, spiral in shape on most radioles (although difficult to determine shape in small eyes). Dorsal lips with radiolar appendages as long as two thoracic chaetigers; with three dorsal pinnular appendages each. Caruncle absent. Low smooth keel (thickened and non-lamellate) projecting ventrally between dorsal lips, arising from raised triangular mound situated mid dorsal to dorsal lips. Ventral lips rounded and well developed; parallel lamellae and ventral sacs present (Fig. 2D). Posterior peristomial collar fused mediadorsally to the faecal groove, with short dorsal lappets equal in length to lateral collar margins, and with shallow dorsolateral U-shaped incisions on both sides forming deep pockets, reaching to second chaetiger (Fig. 2C); lateral collar margins smooth, and ventrally forming overlapping lappets with rounded anterior margins (Fig. 2D). Ventral shields quadrangular, separated from the neuropodial tori, all similar in width. First ventral shield longer than the rest, with m-shaped anterior margin (Fig. 2D). First chaetiger with superior and inferior elongate narrowly hooded notochaetae; superior longer than inferior. Rest of thoracic chaetigers with about 20 elongate narrowly hooded superior chaetae and several irregular rows of broadly hooded inferior notochaetae progressively tapering distally (type B) (Fig. 3A), in fascicles separated by large lamellate interramal lobe. Neuropodial tori slightly diminishing in width posteriorly. Uncini with around 13 rows of small and similarly sized teeth above main fang (Fig. 3D), well



Figure 2. Photographs. (A–E) *Megalomma phyllisae* n.sp., holotype AM W13643: (A) anterior thoracic chaetiger and branchial crown, lateral view; (B) subdistal compound eye in dorsal most radiole; (C) posterior peristomial ring collar and anterior thoracic chaetigers, dorsal view; (D) same, ventral view; (E) posterior abdominal chaetiger and pygidium, dorsal view. (F–I) *Megalomma trioculatum* (paratype, USNM 38409): (F) radiolar crown and anterior segments, lateral view; (G) dorsal collar margins; (H) ventral lappets and anterior segments, lateral view; (I) dorsal most radiole with compound subdistal eye. (J–M) *Megalomma interrupta* n.sp. [Continued on facing page...]

developed breast, handle about 3.5 times the length of the distance from breast to main fang (Fig. 4A). Companion chaetae with asymmetrical membrane with most of surface covered with fine teeth (Fig. 3B,C). Abdominal neuropodia with slender broadly hooded chaetae (Fig. 3F,G). Abdominal notopodial uncini with crest of teeth similar to thoracic uncini (Fig. 3E) but with handles half the length of thoracic ones (Fig. 4B). Pygidium damaged (Fig. 2E). Tough chitinous tube present, embedded externally with shell fragments.

Colour pattern. Body unpigmented, radioles purple, with around three-four irregular broad transverse bands; proximal band most intense and largest, with more irregular patches distally on radioles (Fig. 2A).

Variation. Complete paratype, 95 mm long, 6 mm wide, with eight thoracic and 120 abdominal chaetigers; pygidium damaged. Branchial crown with 30 pairs radioles, 24 pairs with eyes. Incomplete paratype, with eight thoracic and c. 10 abdominal chaetigers. Branchial crown with 25 and 27 radioles in right and left lobes; with subdistal eyes missing from ventralmost 5–7 pairs of radioles. Colour pattern similar in all three specimens.

Reproductive features. Incomplete paratype with oocytes in the ten anterior abdominal segments (rest of abdominal chaetigers missing).

Etymology. The name of this species is given in dedication to Dr Phyllis Knight-Jones in recognition of her great contribution to sabellid taxonomy.

Remarks. This new species shares some characters with others described from the Indo-Pacific: *M. suspiciens* (Ehlers, 1904) recorded from New Zealand, and *M. multioculatum* Fitzhugh, 2002, from Thailand. These characters are the dorsal margins of collar fused to the faecal groove, dorsolateral collar pockets present, and subdistal eyes present on most branchial radioles.

Megalomma phyllisae n.sp. and *M. suspiciens* (Ehlers, 1904) both possess the same type of inferior thoracic chaetae (type B) as well as long-handled thoracic uncini. Furthermore, they share the presence of a smooth, rounded and dorsoventrally-directed “keel” between the dorsal lips, a feature observed after examining the types of *M. suspiciens* and which Tovar-Hernández & Salazar-Vallejo (2008) misinterpreted as a caruncle (p. 1957). Both taxa also lack interramal “eyespot” although they were recorded as present in *M. suspiciens* by Tovar-Hernández & Salazar-Vallejo (2008 p. 1957), probably mistakenly, as they subsequently state these are absent on p. 1961. *Megalomma phyllisae* n.sp. possesses eyes on most of the radioles but in *M. suspiciens* they are only present in 8–9 of 16–18 pairs of radioles (less than half) and the eyes are smaller in the new species. Collar margins have more shallow dorsolateral incisions and deeper pockets compared with those of *M. suspiciens*, and short dorsal lappets are present in *M. phyllisae* n.sp.

and absent in *M. suspiciens*. The new species differs from *M. suspiciens* in the length of the thoracic uncini handles, with approximately 3.5 times the length of the distance from main fang to breast in *M. phyllisae* n.sp., compared with about twice the length from breast to fang in *M. suspiciens* (Fig. 4K), and also in the length of abdominal uncini handles (Figs 4B,L). Other minor differences include the presence of three pinnular appendages per dorsal lip in *M. phyllisae* n.sp. compared with a single pinnular appendage in *M. suspiciens*, the development of the ventral lappets which are long and overlapping in *M. phyllisae* n.sp. and short and non-overlapping in *M. suspiciens*, and the relative position of the thoracic ventral shields to the neuropodial tori with obvious gaps between tori and shields in *M. phyllisae* n.sp. and which abut in *M. suspiciens*.

Megalomma phyllisae n.sp. and *M. multioculatum* differ by the shape of the inferior thoracic notochaetae type B in the new species and type A in *M. multioculatum*). Other differences include the number of rows of cells in the radiole structure, with more than 25 in *M. phyllisae* n.sp. whereas there are four rows of cells in *M. multioculatum*; and the development of dorsal lappets, low in *M. phyllisae* n.sp. and absent in *M. multioculatum*.

Another species recorded in the Indo-Pacific that shares similar features is *M. trioculatum* Reish, 1968, from Marshall Islands, but after reviewing the paratypes (Fig. 2F–I) there is no doubt that there is a misinterpretation of morphology in the original description of this species. The dorsal margins of collar are clearly separated from the faecal groove, ending laterally and abruptly, and not producing any pockets on the sides (Fig. 2G). Therefore, *M. trioculatum* should now be included with those from Knight-Jones’ Group 2C (Table 2). *Megalomma phyllisae* n.sp. also is distinguished from *M. trioculatum* in the shape of the ventral lappets, rounded in *M. phyllisae* n.sp. and pointed in *M. trioculatum* (Fig. 2F,H), and in the length of the thoracic uncini handles (which are much shorter in *M. trioculatum*). Also, the relative number of radiolar eyes is greater in *M. trioculatum* as all radioles of the described holotype and the two paratypes examined possess subdistal eyes in all radioles. The number of rows in the radiolar skeleton of *M. phyllisae* n.sp. is higher than in *M. trioculatum* which only bears four (Fig. 5A,G). It also has to be mentioned that *M. trioculatum* does not show three types of eyes, as stated in the original description; the two paratypes examined possess radiolar eyes only, and these are of two sizes, those in dorsalmost radioles are large and almost surrounding the whole radiole (Fig. 2I), whereas the remaining radioles bear small eyes, all similar in size.

Other *Megalomma* species resemble the new species in the shape of collar dorsal margins and the presence of eyes in most radioles. Some of these species can be distinguished from *M. phyllisae* n.sp. by the presence of a caruncle, absent in the new species. These are *M. lobiferum* (Ehlers, 1904) and *M. carunculata* Tovar-Hernández & Salazar-Vallejo, 2008. The new species has short dorsal lappets equal in length to lateral collar margins, while other species possess long dorsal

Figure 2 [continued from facing page]. ... (paratype AM W3548 except L, AM W35479): (J) radiolar crown, ventral view; (K) detail of radiolar eyes; (L) thoracic and anterior abdominal chaetigers, ventral view; (M) posterior peristomial ring collar and anterior thoracic chaetigers, dorsal view. (N–Q) *Megalomma* sp. 1, AM W30022: (N) anterior segments and base of radiolar crown, ventral view; (O), same, dorsal view; (P) thoracic and anterior abdominal segments, lateral view; (Q) dorsal most radiolar eyes.

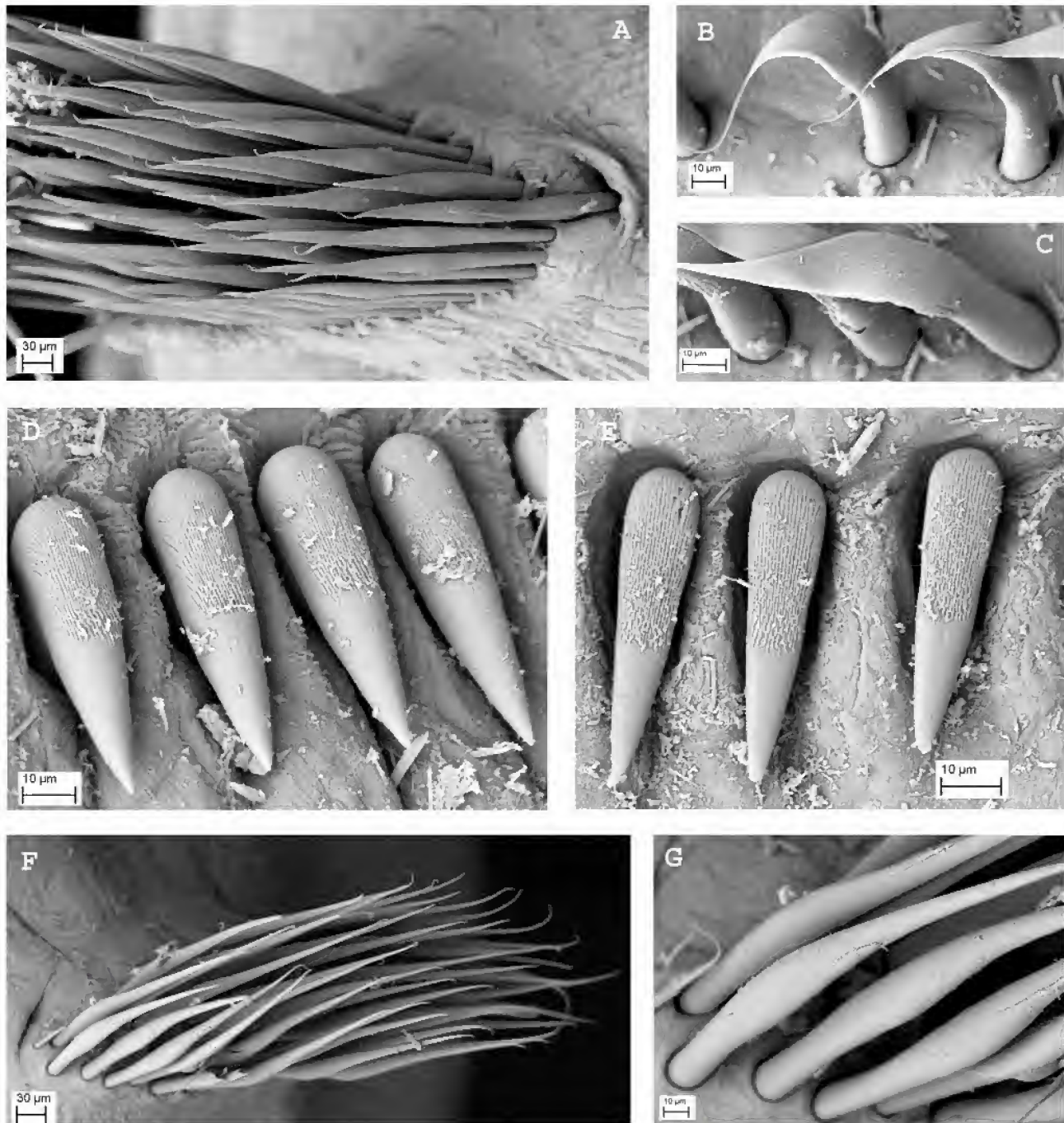


Figure 3. SEM of *Megalomma phyllisae* n.sp., paratype AM W35476: (A) chaetae last thoracic chaetiger, ventral view; (B,C) companion chaetae same chaetiger; (D) uncini same chaetiger; (E) uncini anterior abdominal chaetiger; (F) Anterior abdominal chaetae, dorsal view; (G) detail of inferior abdominal chaetae same chaetiger.

lappets. These are *M. acrophthalmos* (Grube, 1878), *M. fauchaldi* Giangrande *et al.*, 2007, *M. vesiculosum* (Montagu, 1815) and *M. claparedii* (Gravier, 1908) as described by Giangrande and Licciano (2008). *Megalomma phyllisae* n.sp. is distinguished from *M. circumspectum* (Moore, 1923) in the arrangement of radiolar eyes which are lacking in some ventral radioles in the new species and present in all radioles in *M. circumspectum* (Hartman, 1969); thoracic uncini also differ in the two species—uncini handles of *M. phyllisae* n.sp. are approximately twice as long as those of *M. circumspectum*.

***Megalomma cf. acrophthalmos* (Grube, 1878)**

Figs 4C–D, 5B, 6

Sabella acrophthalmos Grube, 1878: page 258, 259.
Megalomma acrophthalmos Knight-Jones, 1997: 316 fig. 2.

Material examined. Western Australia. AM W35477, (1 spec.), Stn WA 621, north west of West Lewis Island, Dampier Archipelago, 20°33'31"S 116°38'13"E, intertidal, coll. P. Hutchings, 26 Jul. 2000. MAGNTW14008, Roebuck Bay, Broome, 19°04'00"S 122°16'59"E, coll. R.J. Hanley and M. Jebb, 29 Aug. 1991 (1 spec. on SEM stub, AM 499).

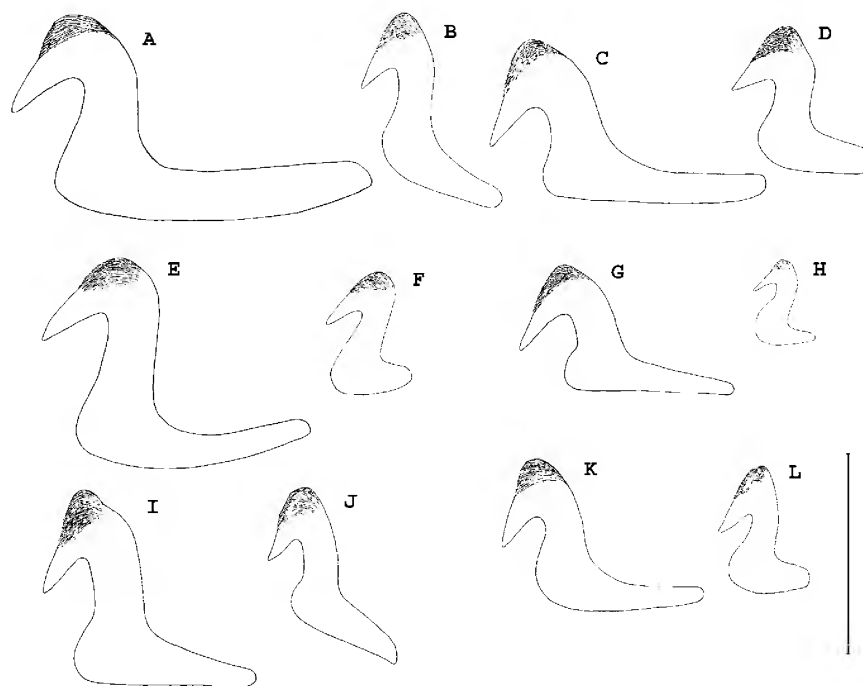


Figure 4. Drawings to scale of thoracic and abdominal uncini. *Megalomma phyllisae* n.sp.: (A) thoracic uncinus; (B) abdominal uncinus. *Megalomma* cf. *acrophthalmos*: (C) thoracic uncinus; (D) abdominal uncinus. *Megalomma interrupta* n.sp.: (E) thoracic uncinus; (F) abdominal uncinus. *Megalomma inflata* n.sp.: (G) thoracic uncinus; (H) abdominal uncinus. *Megalomma* sp. 1: (I) thoracic uncinus; (J) abdominal uncinus. *Megalomma suspiciens*: (K) thoracic uncinus; (L) abdominal uncinus. Scale: 0.1 mm.

Description. Largest specimen AM W35477, 30 mm long, 4 mm wide with eight thoracic and 108 abdominal chaetigers (smallest has eight thoracic and 53 abdominal chaetigers). Crown longer than thorax, 9 mm long, with 25 pairs radioles (15 pairs in the small specimen). Outer surface of radioles quadrangular at the base (Fig. 6B) and rounded distally, with tips shorter than pinnules. Radiolar skeleton composed of 15–20 cells in transverse section (Fig. 5B). Most radioles with subdistal eyes, dorsalmost four pairs appear spiral, and lateral ones large and becoming smaller more ventrally, lacking or missing in 1–2 pairs ventralmost radioles. Dorsal lips with radiolar appendages as long as two thoracic chaetigers, pinnular appendages absent. Caruncle absent. Low smooth keel (thickened and non-lamellate) projecting ventrally between dorsal lips, arising from raised triangular mound situated mid dorsal to dorsal lips. Ventral lips rounded and well developed; ventral parallel lamellae and sacs present. Posterior peristomial collar fused mediodorsally to the faecal groove; dorsal lappets present, elongate and spatulate-shaped distally, as long as lateral collar margins, and with dorsolateral U-shaped indentations on both sides forming pockets, reaching to level of second chaetiger (Fig. 6A); lateral collar margins smooth (Fig. 6B), and ventrally forming overlapping lappets with rounded anterior margins, with a complete midventral incision (Fig. 6C). Ventral shields rectangular, all separate from the neuropodial tori (Fig. 6C), all similar in width. First ventral shield longer than the rest, with m-shaped anterior margin. First chaetiger with superior and inferior elongate narrowly hooded notochaetae; superior longer than inferior (Fig. 6D). Rest of thoracic chaetigers with two rows of superior elongate narrowly hooded and

two rows of inferior broadly hooded notochaetae with progressively tapering tips (type B) (Fig. 6E); lamella-like lobe present between superior and inferior notochaetal fascicles. Uncini with around 7–10 rows of small, similarly sized teeth above main fang (Fig. 6F,G), well developed breast, handle long, three times the length of the distance from breast to main fang (Fig. 4C). Companion chaetae with asymmetrical membrane (Fig. 6H). Abdominal neuropodia with slender broadly hooded chaetae (Fig. 6I). Abdominal uncini similar to thoracic uncini, with similarly-sized teeth over the main fang but covering more surface area (Fig. 6J) and with shorter handle (Fig. 4D). Pygidium with four small lobes, scattered eyespots laterally.

Colour pattern. Three regular transverse pigment bands on branchial radioles plus other less regular pigment on pinnules distally. Brown pigment present on anterior dorsum of body and with dark regular patches dorsolaterally on anterior margins of first seven thoracic segments.

Remarks. Of the species recorded in the Indo-Pacific, these described specimens most closely resemble *M. multioculatum* and *M. phyllisae* n.sp. in the presence of subdistal eyes on most radioles and with dorsal margins of collar fused to the faecal groove. However, *M. cf. acrophthalmos* has conspicuous elongated dorsal collar lappets which are absent in *M. multioculatum* and *M. phyllisae* n.sp. These three features (pattern of distribution of radiolar eyes, fusion and shape of collar dorsal margins), are shared with the type material described from the Philippines (Grube 1878) and restudied and drawn by Knight-Jones (1997). The chaetae and uncini of specimens from both

localities also show similarities: the inferior thoracic chaetae are broadly hooded but with a progressively-tapering hood (type B) and the thoracic uncini have long handles, exceeding twice the distance of main fang to breast. The only specimen available from the type locality (most probably the holotype according to Knight-Jones [1997]) is not in good condition. Because of this reason, identification should be confirmed with additional material from the type locality. However, it is quite possible that the species has a southeast Asian distribution. This species has also been recorded in Sri Lanka (Willey, 1905) as *Branchiomma acrophthalmos* but this identification has not been confirmed.

Other species in the genus described as possessing well developed dorsal lappets are *M. fauchaldi* (Giangrande *et al.*, 2007) from Belize, *M. vesiculosum* from England, and *M. mushaense* and *M. nechamae* from the Red Sea, all of which also possess radiolar eyes on most radioles, collar fused to the faecal groove and pockets present, although this last feature was not interpreted as such by Knight-Jones (1997). The shape and size of the lappets and the margin of the collar of *M. acrophthalmos* are all different in shape and size to these four species, and their geographical distributions are discrete and separated widely enough to also separate them as different species.

Megalomma interrupta n.sp.

Figs 2J–L, 4E–F, 5B, 7, 8

Material examined. Queensland. HOLOTYPE AM W35478, One Tree Island, 23°30'S 152°05'E, Stn 10.4, coll. P.A. Hutchings, Oct. 1972. PARATYPES: AM W35479, (6 spec., 1 on SEM stub AM 501), same locality as holotype; AM W35480 (1 spec.), Stn 11.2, same locality and date; AM W35481 (1 spec.), Stn 1.1, same locality and date; AM W35482 (1 spec.), Stn 5.4, same locality and date; AM W35483 (2 spec.), Stn 14.3, same locality and date; AM W35484 (1 spec.), Stn 2.4, same locality and date; AM W35485 (2 spec.), Stn 10.2, same locality and date; AM W35486 (1 spec.), Stn 15.1, same locality and date; AM W35487 (1 spec.), Stn 5.1, same locality and date; AM W35488 (5 spec., 2 on SEM stubs MI090–91), Stn 10.3, same locality and date; AM W35489 (1 spec.), Stn 7.1, same locality and date; AM W35490 (1 spec.), off Station Beach, Lizard Island, 14°41'S 145°27'E, 75 LIZ 1–8, coll. P.B. Berents & P. Hutchings, 6 Jan. 1975, from dead *Pocillopora*, 3 m; AM W35491 (3 spec., one on SEM stub), south headland of Turtle Beach, Lizard Island, 14°39'S 145°27'E, 76 LIZ 21–1, coll. P. Berents & P. Hutchings, 27 Aug. 1976, dead branching coral, 3 m; AM W35492 (1 spec.) off Granite Bluff, Lizard Island, 14°39'S 145°27'E, 76 LIZ 27–1, coll. P. Berents & P. Hutchings, 31 Aug. 1976, thin plates dead coral, 6 m; AM W35493 (2 spec.), off Coconut Beach, Lizard Island, 14°41'S 145°28'27"E, QLD1185, coll. K.B. Attwood & P.A. Hutchings, 29 Mar. 1995, dead coral at foot of reef, covered in *Lithothamnion*, 12 m; AM W35494 (1 spec.), reef front between Bird & South Islands, Lizard Island, 14°41'53"S 145°27'51"E, QLD1187, coll. P.A. Hutchings, 30 Mar 1995, dead coral, 13 m; AM W35495 (1 spec.), off North Point Lizard Island, 14°38'51"S 145°27'12"E, QLD1183, coll. P.A. Hutchings, 28 Mar. 1995, dead coral with heavy coralline algal growth, 20 m. **Western Australia.** AM W35496 (2 spec.), Kendrew Island, Dampier Archipelago, 20°28'42"S 116°32'E, coll. P.A. Hutchings, 3 Apr. 1987, crevice fauna, 10 m; AM W35497 (1 spec.), 2 km west of Angel Island, Dampier Archipelago, 20°29'46"S 116°47'29"E, WA 639, coll. P.A. Hutchings & L. Avery, 4 Aug. 2000, pinnacle, dead coral substrate & large bivalves heavily encrusted and bored, 10 m; AM W35498 (3 spec., 2 on SEM stub MI089 and MI090), west of Angel Island, 20°29'03"S 116°47'50"E, WA619, coll. P.A. Hutchings & L. Avery, 25 Jul. 2000, dead coral, 6 m; AM W35499 (2 spec.), East Montlivet Island, Kimberley region, 15°06'S 125°18'E, Stn 50, coll. P.A. Hutchings, 16 Jul. 1988, 6 m; AM W35500 (1 spec.), south side of Long Reef, Kimberley region, 14°01'S 125°44'E, Stn 60, coll. P.A. Hutchings, 18 Jul. 1988, 20 m. **Indonesia.** MAGNT W5975 (1 spec., Bay of Maumere, Pasir Sari, 8°37'00"N 122°13'59"E, 24–27 m, rubble E, coll. B.C. Russell, 6 Nov. 1991.

Additional material. Queensland (identification is tentative due to poor preservation): AM W198006 (2 specimens, 1 on SEM stub MI086), Calliope River, Gladstone, 23°51'S 151°10'E, coarse sand, 3.9 m, coll. P. Saenger, Aug. 1982; AM W198007 (1 spec.), same locality and date, silty sand, 5.6 m.

Diagnosis. This species is characterized by a combination of features: radiolar eyes present in dorsalmost and lateral radioles only, with approximately four radioles in between without eyes; radiolar skeleton with approximately 10 cells in cross section; collar margins not fused to the faecal groove, shallow inconspicuous pockets present, caruncle absent, and inferior thoracic broadly hooded chaetae with distal end narrowing abruptly (type A).

Description. Holotype 22 mm long and 2.5 mm wide with body flattened dorsoventrally, thorax wider than abdomen and abdominal segments diminishing in size posteriorly. Eight thoracic and 78 abdominal chaetigers. Crown longer than thorax, with 15 radioles in each lobe semicircular lobe. External margin of radioles quadrangular at the base (Figs 2I, 7C) and rounded towards the tips, without lateral flanges but with two longitudinal bands of cilia. Tips of radioles tapering, shorter than pinnules (Fig. 2J). Basal membrane absent. Radiolar skeleton with about 10 cells in transverse section at the base of radioles (Fig. 5C). Dorsalmost pair of radioles longer than the rest, each with a large subdistal compound eye almost surrounding the whole radiole, and with visible ommatidia (Figs 2J, 7K), adjacent next five pairs of radioles without eyes, next two pairs of lateral radioles with small, similarly-sized subdistal eyes. Dorsal lips with radiolar appendages as long as two thoracic chaetigers, with lateral lamellae almost reaching the tip of appendage; three dorsal pinnular appendages each. Caruncle absent. Ventral lips rounded and well developed. Ventral sacs and parallel lamellae present (Fig. 7A). Collar with pointed ventral lappets (Figs 2I, 7A); lateral margins of collar smooth with dorsolateral U-shaped indentations on both sides forming inconspicuous pockets and continuing as ridges to the middorsal faecal groove (Figs 2I, 7B–C). Ventral shields quadrangular with parallel lateral margins, not in contact with the neuropodial tori (Figs 2K, 7A). First ventral shield longer than the rest, with a midanterior incision (m-shaped anterior margin). First chaetiger with superior and inferior elongate narrowly hooded notochaetae; superior row longer than the inferior one (Fig. 7D). Rest of thoracic chaetigers with superior elongate narrowly hooded and inferior broadly hooded notochaetae (about 20, type A) arranged in two rows (Fig. 7H). Notopodia of thoracic chaetigers with elongated lobe between superior and inferior chaetae (Fig. 7B). Neuropodial tori becoming slightly shorter more posteriorly. Thoracic uncini with several rows of small teeth, all similar in size above main fang (Fig. 7F,G); uncinus with well developed breast and handle about twice the length of the distance from breast to main fang (Fig. 4E). Companion chaetae with asymmetrical membrane covered proximally with rows of small teeth (Fig. 7E). Abdominal neuropodia with elongate, broadly hooded chaetae arranged in two rows (Fig. 7I). Notopodial abdominal uncini similar to the thoracic (Fig. 7J) but with shorter handle (Fig. 4F). Pygidium as a rounded papilla without pygidial eyes.

Variation. There is some variability in the number of thoracic chaetigers, with some paratypes having nine or ten. The number of radioles varies between 10 and 18 pairs and

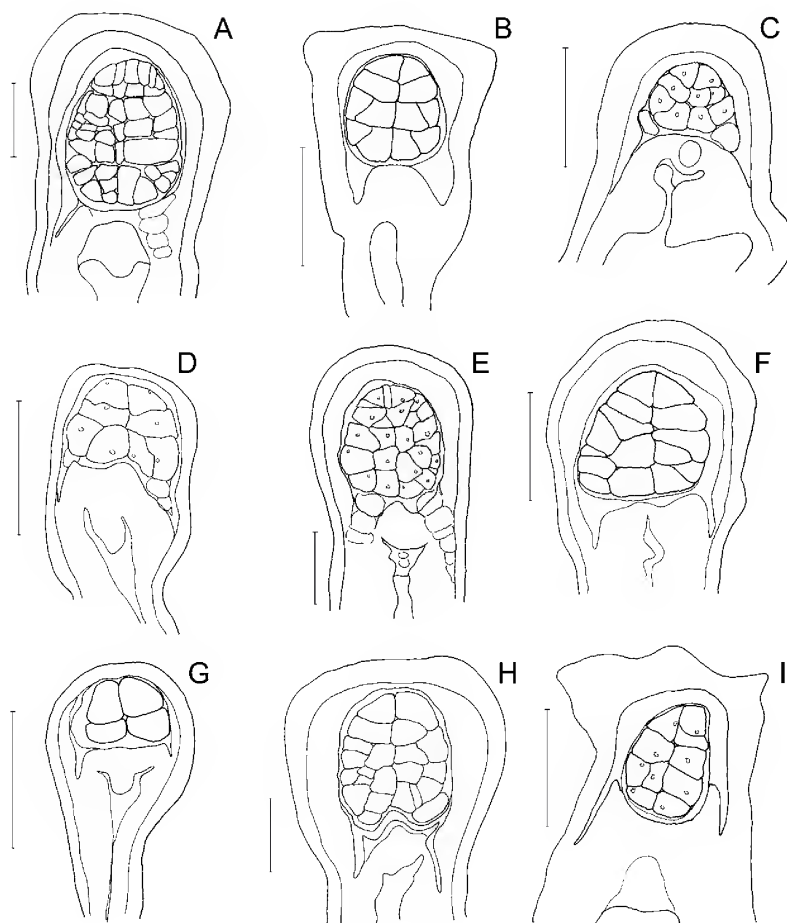


Figure 5. Drawings to scale of radiolar sections, at the base: (A) *Megalomma phyllisae* n.sp.; (B) *M. interrupta* n.sp.; (C) *M. cf. miyukiae*; (D) *M. inflata* n.sp.; (E) *Megalomma* sp. 1; (F) *M. quadrioculatum*; (G) *M. trioculatum*; (H) *M. lanigera*; (I) *M. suspiciens*. Scale: 0.1 mm.

the number of compound subdistal eyes also differs among specimens and is not related to the number of radiolar cells (Table 1, Fig. 9). All specimens share the same arrangement of a large radiolar eye on each of the dorsalmost radiolar cells, but the small, similarly-sized subdistal radiolar eyes on a few lateral radiolar cells can be absent entirely from some specimens. Dorsal lips bear long radiolar appendages that in some specimens reach the length of four thoracic chaetigers. In all specimens the peristomial collar has dorsal margins separated from the faecal groove, but in some specimens under the dissecting microscope, it is not clear whether pockets are absent or present, as some specimens exhibit low membranes as continuations of the dorsal margins of the collar which could be considered as vestigial pockets (according to Knight-Jones, 1997) (see Fig. 2M), a feature that is made very clear using scanning electron microscopy (see Fig. 7B,C). Also, the ventral lappets of the collar may be observed as overlapping or not, depending on whether they are erect or folded back. Specimens show variability in the size of the gap between ventral shields and thoracic tori, even within the same sample. In some specimens (e.g., holotype, paratypes, and AM W35498) shields and tori are separated by a wide gap, in others (e.g., AM W35496) they are separated only in posterior chaetigers, while in other specimens they are in contact in all chaetigers (e.g., AM W35497).

After observing the variability within this morphospecies under both dissecting and compound microscopes, some specimens were selected from several different localities covering the species' distribution and which also displayed the variability in the distribution of radiolar eyes, and these were studied under SEM. Thoracic and abdominal chaetae appear to be similar in shape, size and arrangement within their fascicles (Fig. 8B,C,F,G,J,M,N) but variability was observed among thoracic and abdominal uncini (Fig. 8A,D,E,H,I,K,L,O). All specimens have similarly-sized teeth covering half the surface of the main fang in thoracic uncini, and a slightly greater surface area of abdominal uncini, but some specimens show relatively larger teeth (Fig. 7A,D,E,H,I,K) than others (Fig. 8L,O); however these differences do not seem to be correlated with the specimens' differing geographical localities, as variability is observed among specimens from the same sample. Until further studies reveal if this is, in fact, a complex of species that coexist in the same habitats in the same localities, we consider this variability to be intraspecific.

Colour pattern. The intensity of the pigmentation varies among the specimens and could be due to different methods or lengths of time of preservation. The specimens from Western Australia are more pigmented in general than those

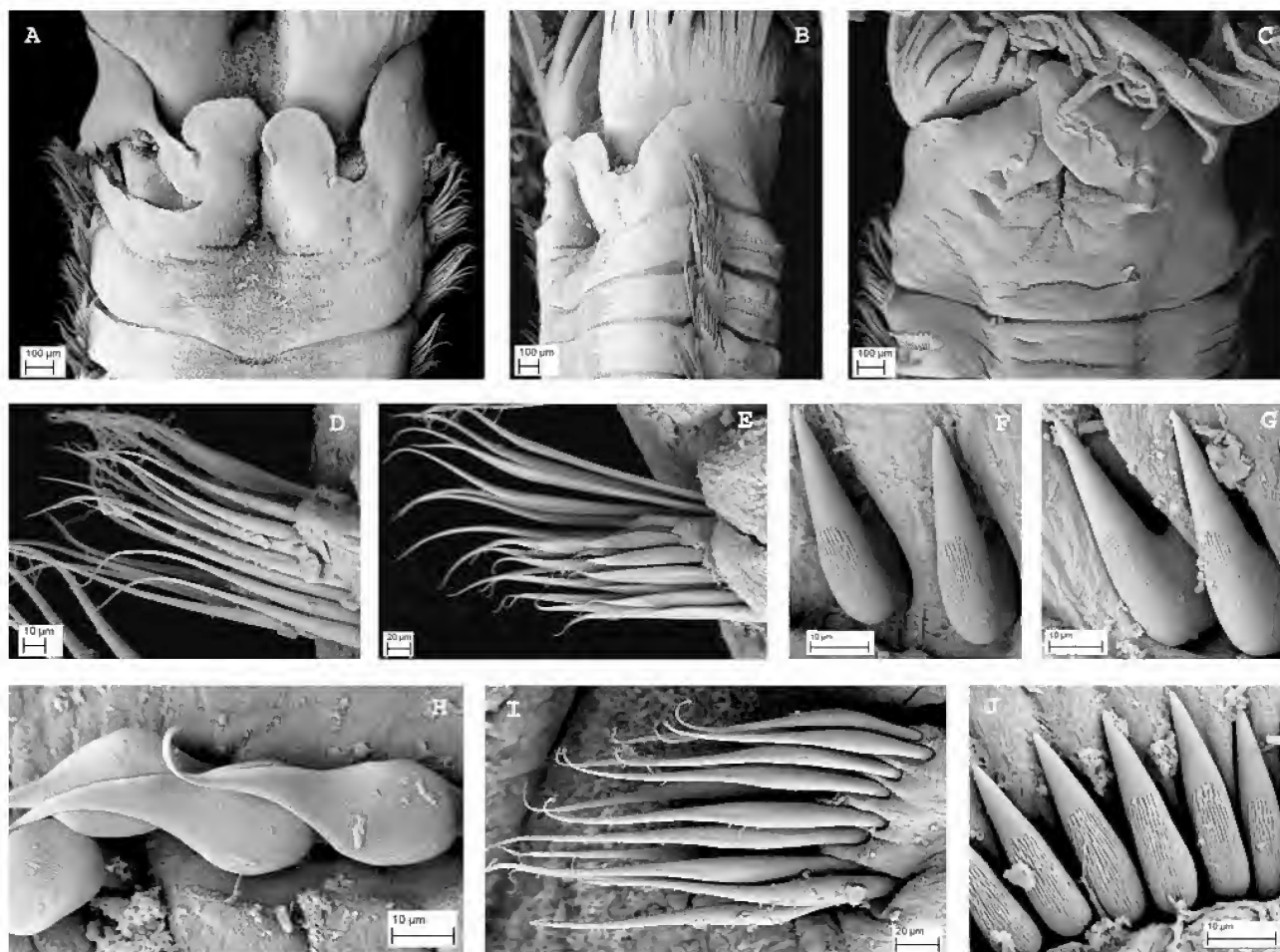


Figure 6. SEM of *Megalomma* cf. *acrophthalmos*, MAGNT W14008. (A) dorsal collar margins with dorsal lappets; (B) lateral collar margins and anterior thoracic chaetigers, lateral view; (C) anterior collar margins and ventral lappets; (D) chaetae first thoracic chaetiger, ventral view; (E) chaetae of second thoracic chaetiger, ventral view; (F) uncini, same segment; (G) uncini last thoracic segment; (H) companion chaetae posterior thoracic chaetiger; (I) chaetae, anterior abdominal segment; (J) uncini, same chaetiger.

from Queensland (Figs 2J–M). The thorax is anteriorly pigmented, particularly dorsally and ventrally around tori. The base of the branchial crown is also pigmented, there is a longitudinal medial line basally on each radiole, and some specimens also exhibit irregular, variable-width, transverse bands of pigment on the crown.

Etymology. The name of this species refers to the discontinuous arrangement of eyes on the radioles.

Remarks. These specimens do not fit into the classification proposed by Knight-Jones (1997) as her categories do not consider the combination of the following features: dorsal margins of collar not fused to the faecal groove, pockets present and compound eyes in dorsalmost and also in some lateral radioles. These characters, common to all these specimens, justify the inclusion of a new category (called Group 2E herein) in Knight-Jones' classification. The collar pockets could be considered as vestigial or even absent in some specimens and therefore this species should also be compared with those previously placed in the categories 2B, 2C and 2D which also lack dorsolateral collar pockets. The new species resembles *M. messapicum* Giangrande & Licciano, 2008, from the Mediterranean, in the particular arrangement of compound subdistal radiolar eyes, with

a large eye almost surrounding the tip of the dorsalmost radioles, as well as some lateral radioles bearing small, similarly-sized subdistal radiolar eyes, and with those radioles between the dorsalmost and lateral ones lacking eyes (see Table 1). These two species, confined to distant and isolated geographic areas, are distinguished by the difference in the degree of fusion of collar margins with the faecal groove, separated in *M. interrupta* n.sp. and fused in *M. messapicum*; moreover *M. interrupta* n.sp. is characterized by the presence of large interramal lobes in thoracic notopodia and a radiolar skeleton with around 10 cells in transverse section, whereas *M. messapicum* does not possess enlarged interramal notopodial lobes, and has a radiolar skeleton of four cells in cross-section (Giangrande, pers. comm.).

Megalomma cf. *miyukiae* Nishi, 1998

Figs 5C, 10

Megalomma miyukiae Nishi, 1998: 53–59, figs 1–4.

Material examined. Northern Territory. MAGNT W331 (1 spec.), Coral Bay, Port Essington, 11°11'50"S 132°02'55"E, collected by D. Staples, 17 May 1983, broken reef, 3–5 m; MAGNT W17354 (1 anterior

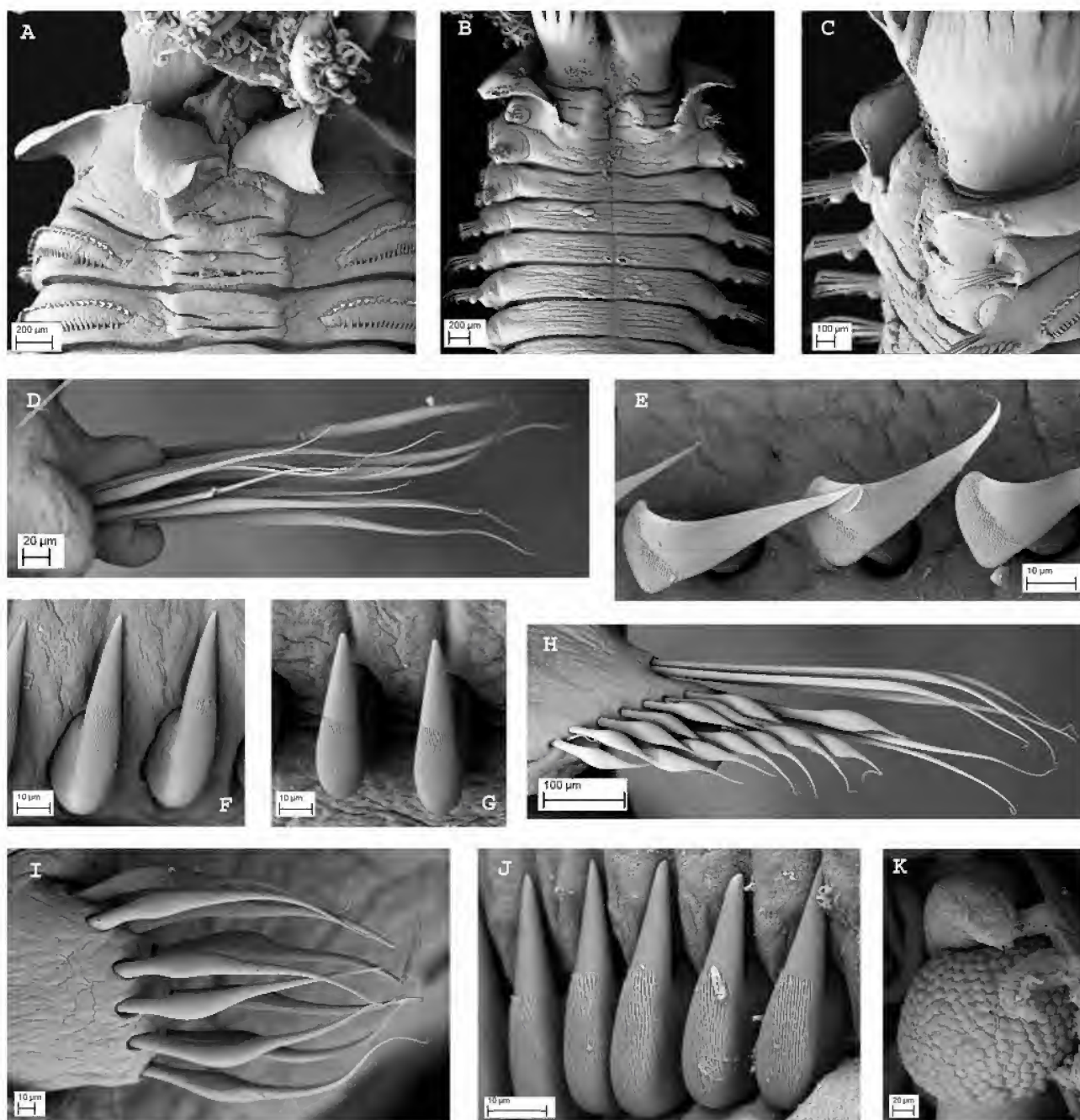


Figure 7. SEM of *Megalomma interrupta* n.sp. paratype, AM W35479. (A) anterior thoracic chaetiger and posterior peristomial ring collar, ventral view; (B) same, dorsal view; (C) thorax and branchial crown junction, showing dorsal collar margins, lateral view; (D) chaetae fascicle, first thoracic chaetiger, ventral view; (E) companion chaetae, second thoracic chaetiger; (F) uncini, same chaetiger; (G) uncini, last thoracic chaetiger; (H) last thoracic notochaetal fascicle, ventral view; (I) anterior abdominal neurochaetal fascicle, ventral view; (J) anterior abdominal uncini; (K) subdistal compound radiolar eye.

end on SEM stub, crown in vial), Cullen Bay Marina, Darwin Harbour, 12°27'09"S 130°49'18"E, coll. CSIRO CRIMP survey team, 30 Mar. 1999; MAGNT W17355 (1 detached crown only), same site and collectors; MAGNT W17356 (1 spec.), Inner Stokes Hill Wharf, Darwin Harbour, S12°28'13"S E130°50'59"E, coll. CSIRO CRIMP survey team, 16 Aug. 1999. **Queensland.** AM W35502 (1 crown + spec. on SEM stub), Lorim Point Wharf, Weipa, 12°40'S 141°57'E, P990 W1, coll. CRC Reef Research Centre Ltd, Oct. 1999, from pile scraping, 7 m.

Description. Only one specimen (MAGNT W331) complete, the rest are missing posteriors or in poor condition (branchial crown is detached from body). Complete specimen with 10 thoracic and 120 abdominal chaetigers. Crown with

18 radioles on each semicircular lobe. External margin of radioles rounded, without lateral flanges. Tip of radioles digitiform and longer than distal pinnules, except radioles bearing compound eyes, where tip is shorter. Radiolar skeleton with 8–10 rows of cells (Fig. 5C). Three pairs of dorsalmost radioles with subdistal compound eye, with distinct ommatidia, diminishing in size ventrally and with dorsalmost pair of eyes almost surrounding the radiole, leaving a small gap on the outer margin. Dorsal lips with radiolar appendages as long as two thoracic chaetigers. Ventral lips rounded and well developed. Parallel lamellae

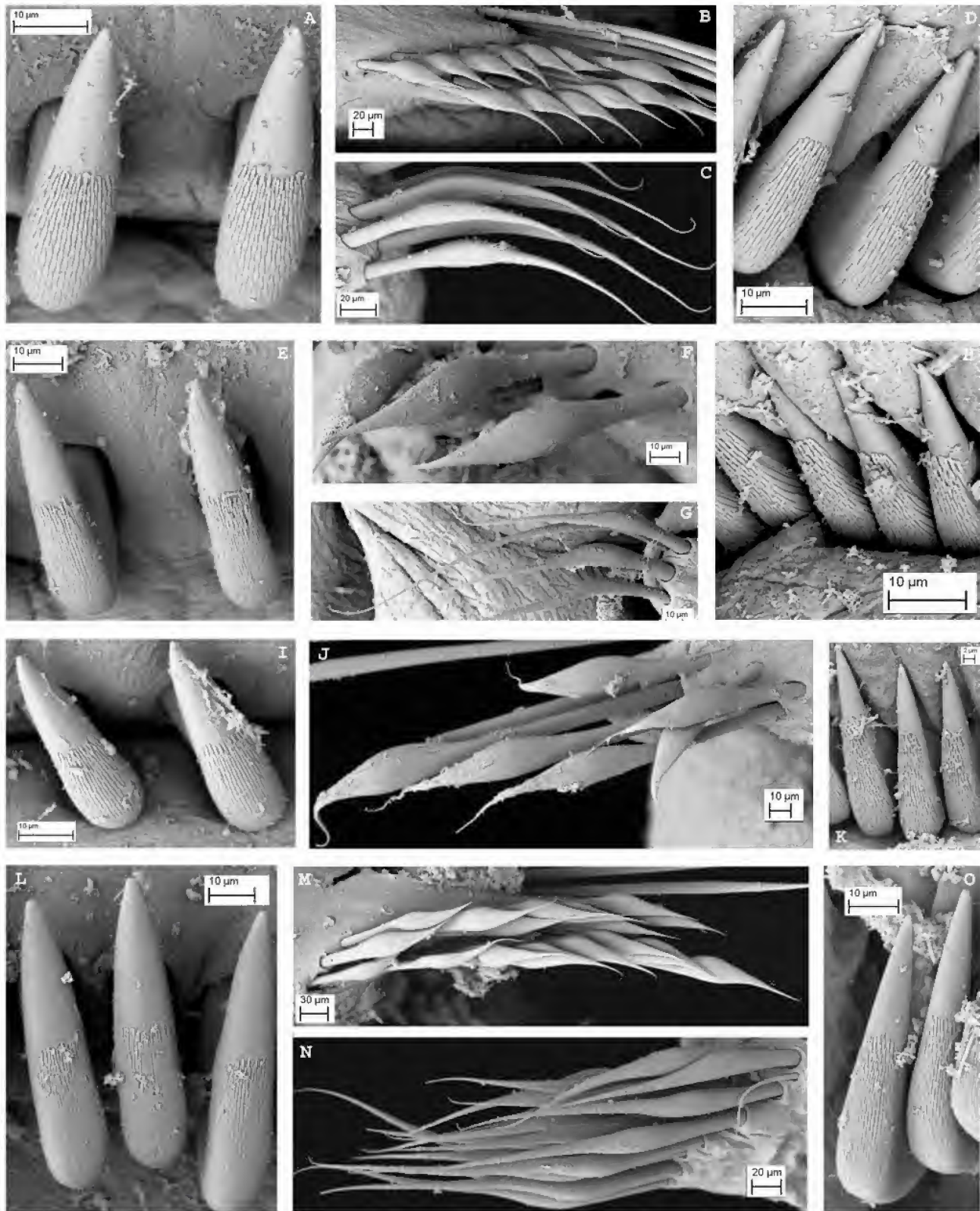
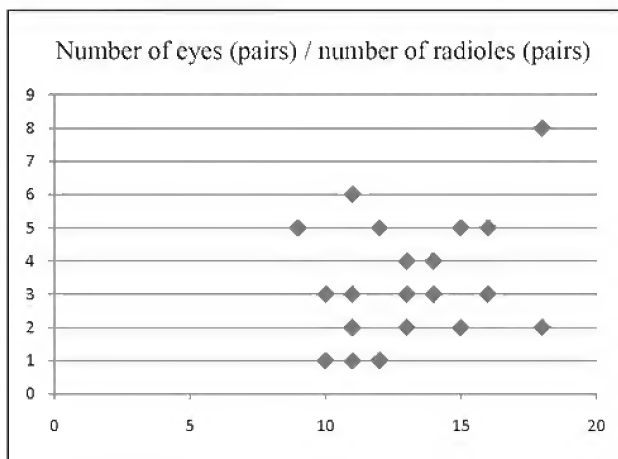


Figure 8. SEM of *Megalomma interrupta* n.sp. (A–D) AM W35490, from Lizard Island (QLD): (A) uncini, third thoracic chaetiger; (B) inferior notochaetae, fifth thoracic chaetiger, ventral view; (C) anterior abdominal neurochaetae, ventral view; (D) anterior abdominal uncini. (E–H) AM W35488, from One Tree Island (QLD), with radiolar eyes on dorsalmost pairs of radioles: (E) thoracic uncini; (F) thoracic inferior notochaetae, ventral view; (G) anterior abdominal neurochaetae, ventral view; (H) anterior abdominal uncini. (I–K) AM W35488 from One Tree Island (QLD) with several radiolar eyes: (I) thoracic uncini; (J) thoracic inferior notochaetae, ventral view; (K) anterior abdominal uncini. (L–O) AM W35498, specimen from Kimberleys (WA): (L) uncini, third thoracic chaetiger; (M) notochaetae, fourth thoracic chaetiger, ventral view; (N) anterior abdominal neurochaetae; (O) anterior abdominal uncini.

Table 1. Variation of number of chaetigers, pairs of eyes and radioles on *M. interrupta* n.sp.

site	thoracic chaetigers	abdominal chaetigers	number radioles (pairs)	number of eyes (pairs)	distribution of radiolar eyes
AM W35480	8	91	13	2	1, X
AM W35481	8	—	10	3	1, 5, 6
AM W35479	10	—	18	2	1, 5
AM W35479	8	83	16	3	1, 6, 7
AM W35479	10	—	13	4	1, 6–8
AM W35479	8	69	11	6	1, 4–8
AM W35479	8	73	12	1	1
AM W35482	8	>100	16	5	1, 7–10
AM W35483	8	—	14	3	1, 4, 5
AM W35485	8	—	13	4	1, 6–8
AM W35485	8	—	14	3	1, 8, 9
AM W35485	8	c. 100	14	3	1, 8, 9
AM W35486	8	—	9	5	1, 6–9
AM W35487	8	—	12	5	1, 7–10
AM W35488	8	118	10	1	1
AM W35488	8	104	11	2	1, 4
AM W35488	8	81	13	3	1, 8–9
AM W35488	8	—	11	1	1
AM W35488	8	84	11	3	1, 7, 8
AM W35489	8	—	13	4	1, 5–7
AM W35496	8	—	14	4	1, 6–8
AM W35498	9	—	15	5	1, 8–11
AM W35498	9	—	15	2	1, 9
AM W35497	8	—	14	3	1, 5, 6
MAGNT W5975	8	—	18	8	1, 6–12

Figure 9. Graph representing the variety of number of pairs of eyes against the number of pairs of radioles in *Megalomma interrupta* n.sp.

and ventral sacs present (Fig. 10A). Caruncle absent. Smooth keel present between dorsal lips (Fig. 10B). Posterior peristomial collar with rounded dorsal margins and with wide gap between them but with low fleshy ridges that continue obliquely from middorsal faecal groove to vestigial pockets, pockets level with notochaetae of first chaetiger (Fig. 10B); lateral margins of collar smooth, perpendicular to body axis and covering the junction of thorax and crown; ventral lappets prominent, rounded and overlapping (Fig. 10A). Ventral shields quadrangular, all similar in width down

the body, almost in contact with the neuropodial tori (Fig. 10A). First ventral shield longer than the rest, with m-shaped anterior margin although not conspicuous. First chaetiger with about 20 superior and inferior elongate narrowly hooded notochaetae, superior longer than inferior. Chaetigers 2–8 with about 20 elongate narrowly hooded superior chaetae and 20–25 broadly hooded inferior chaetae (Fig. 10C–E) (type B). Neuropodial tori slightly diminishing in width posteriorly. Thoracic uncini with several rows of small teeth, similar in size, above main fang (Fig. 10F); uncinus with well developed breast, handle similar in length to the distance from breast to main fang. Companion chaetae with asymmetrical membrane and small teeth covering most of its surface (Fig. 10H). Neuropodia of anterior abdominal chaetigers with broadly hooded chaetae (Fig. 10I). Abdominal notopodia with uncini similar to thoracic but with shorter handles (Fig. 10G). Pygidium bilobed, eyespots absent. Chitinous hard tube (specimen MAGNT W17356), covered with fine sand on anterior third of length.

Variation. The other specimens have eight thoracic chaetigers and 15–25 radioles on each branchial lobe. Specimens possess one to three pairs of subdistal radiolar eyes, and some have eyes missing on the third dorsalmost radioles, in which case they are present on the fourth pair; relative size of eyes varies from one specimen to another—in some the two dorsalmost pairs are large and the third pair significantly smaller, while in others the difference in size is more gradual, diminishing ventrally. The specimens also vary in the size of the gap between ventral shields and tori. In some specimens the ventral lappets do not overlap.

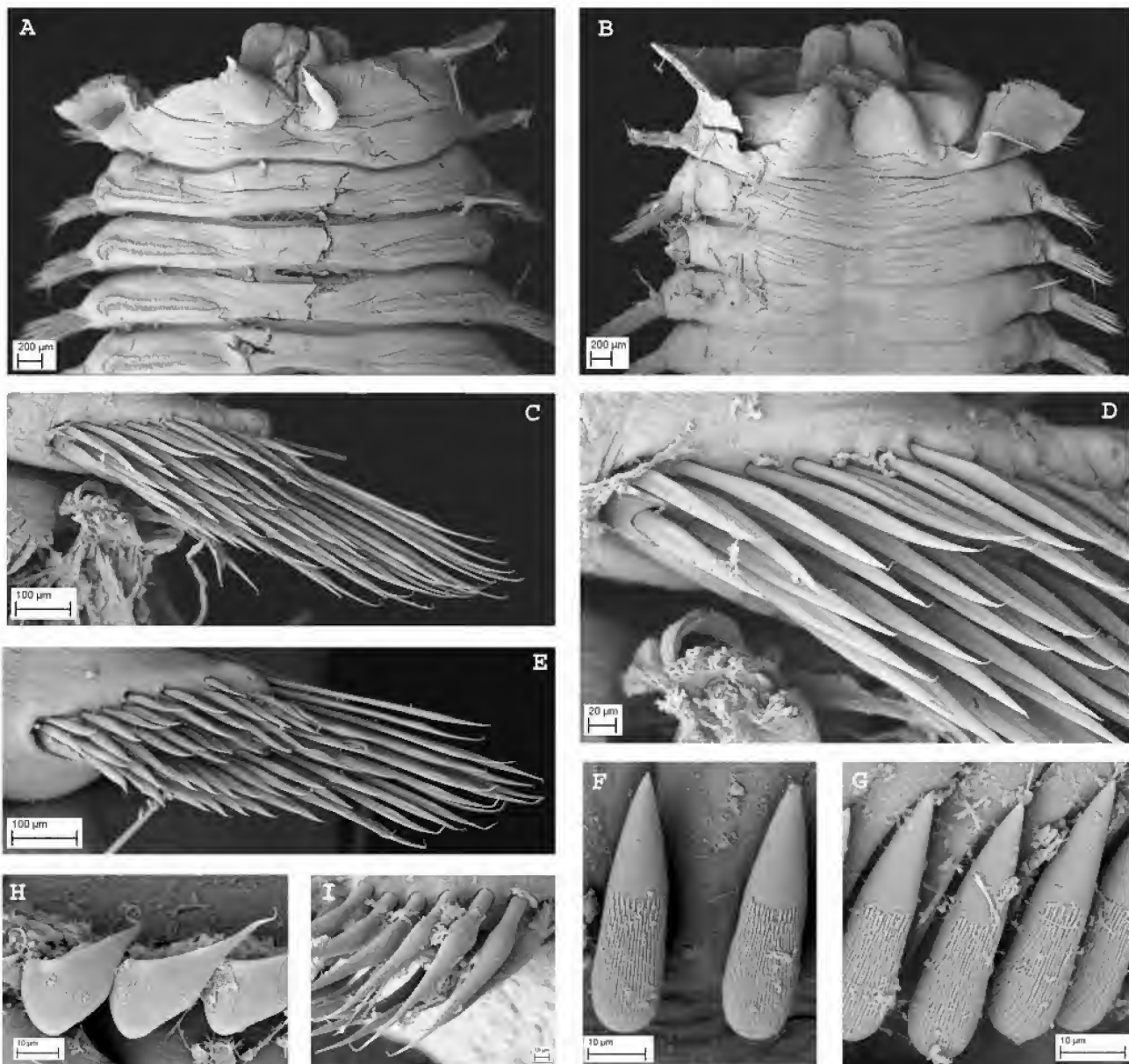


Figure 10. SEM of *Megalomma* cf. *miyukiae*, AM W35502: (A) anterior thoracic chaetiger and posterior peristomial ring collar, ventral view; (B) same, dorsal view; (C) notochaetae, first chaetiger, ventral view; (D) inferior thoracic chaetae, anterior chaetiger, ventral view; (E) whole fascicle; (F) thoracic uncini; (G) abdominal uncini; (H) companion chaetae; (I) anterior abdominal neurochaetal fascicle.

Colour pattern. Body slightly pigmented anteriorly, particularly the collar, ventral shields, and ventral margins of parapodial tori, although tori unpigmented. Base of crown and anterior margin of peristomium dorsally coloured; radioles with some transverse irregular bands and with some pinnules pigmented.

Remarks. The identification of this species in Australia should be confirmed with more material in better condition. Some features, such as separation of the dorsal margins of the collar from the faecal groove, the presence of vestigial pockets of the collar and the presence of subdistal eyes in only a few dorsal radioles agree with the original description of *M. miyukiae*, described from Thailand (Nishi, 1998). But there are some differences between these specimens and the types of *M. miyukiae*. Vestigial pockets of the collar are present on the specimens described herein, and although

we consider this a feature that might be overlooked and interpreted as “pockets absent” when there is no fusion of collar with the faecal groove, Nishi (1998) is aware of the possibility of vestigial pockets being present as he states in Remarks when comparing his new species to others, that *M. heterops* Perkins, 1994, “has vestigial pockets joining ridges and dorsolateral margins”, and mentions that only a “small bulge” is present on *M. miyukiae* specimens. In the absence of examination of type material of *M. miyukiae*, we can only assume that our specimens differ from *M. miyukiae* in this character. The first ventral shield is not as long as twice the length of the following shields, and also radiolar tips are longer than pinnules except for the ones bearing compound subdistal eyes, but these differences could be due to intraspecific variation. These specimens should also be compared with *M. kaikourense*, described from New Zealand, as they share some features such as

dorsal collar margins not fused to faecal groove, presence of vestigial pockets (according to original description by Knight-Jones, 1997), and eyes on dorsalmost radioles. The differences between the two species are that the specimens from Australia bear eyes on other radioles, and also, using a perhaps more significant species-character, that the inferior thoracic chaetae have progressively tapering distal tips (type B) in the specimens described herein, whereas they narrow abruptly (type A) in *M. kaikourense*.

Megalomma inflata n.sp.

Figs 4G,H, 5D, 11

Material examined. New South Wales. HOLOTYPE AM W35503, southeast of Bate Bay, 34°04'S 151°13'E, coll. by The Ecology Lab for RMI/Pioneer Project, 15 Jan. 1990, 45–50 m, Stn RMI C26. PARATYPES: AM W35504 (1 spec.), east of Bass Point, 34°36'S 150°54'E, 25 Jun.–26 Jul. 1990, 45–50 m, Stn RMI BP51; AM W35505 (2 spec.), east of Bass Point, 34°36'S 150°54'E, 3–18 Jan. 1991, 65–70 m, Stn RMI 4/236; AM W35506 (1 spec.), east of Bass Point, 34°36'S 150°54'E, 25 Jun.–26 Jul. 1990, 45–50 m, Stn BP43; AM W23057 (1 spec. on SEM stub), east of Bass Point, 34°36'S 150°54'E, coll. by The Ecology Lab for RMI/Pioneer Project, 1 Feb. 1990, 25–50 m. AM W35753 (1 spec.), south of Batemans Bay, south side of Burrewarra Point, 35°50'16"S 150°14'05"E, 28 Mar. 2004, 17 m, from algal and bryozoan (cf. *Amathia*) turf on vertical rock face, coll. Australian Museum party, Stn NSW 2631.

Additional material. *Megalomma quadrioculatum*, holotype ZMUH PE 1303, Aripu Coral Reef, Sri Lanka, coll. Willey, 1905.

Diagnosis. The synapomorphy of this species is the presence of an inflated peristomium protruding from collar. Moreover, *M. inflata* n.sp. is characterized by a combination of characters: dorsalmost radioles with large subdistal compound eyes and occasionally one or two small pairs in following radioles, radiolar skeleton with around 10 cells in transverse section, dorsal margins of collar fused to the faecal groove forming broad and U-shaped pockets on each side, caruncle absent, and thoracic inferior chaetae with tips progressively tapering (type B).

Description. Holotype complete and in good condition measuring 22 mm long and 2 mm wide, with eight thoracic chaetigers and 37 abdominal chaetigers. Crown longer than thorax, with 14 pairs of radioles arranged in two semi-circular lobes. External margin of radioles quadrangular, lateral flanges absent (Fig. 11A), skeleton with 8–10 cells in transverse section (Fig. 5D). Tip of radioles digitiform and shorter than pinnules (Fig. 11A). Three pairs of dorsalmost radioles with a subdistal compound eye and an extra fourth eye on the right side, with distinct ommatidia, eye-size diminishing ventrally; dorsalmost eyes spiral, almost surrounding radioles. Dorsal lips with radiolar appendages shorter than two thoracic chaetigers and no visible pinnular appendages. Ventral lips rounded and well developed. Ventral sacs present. Caruncle absent. Short smooth keel present. Posterior peristomial collar with rounded dorsal margins fused to faecal groove, dorsal collar lappets absent (Fig. 11C); collar pockets present, low due to deep incision (dorsal peristomium inflated and dorsal collar difficult to discern) (Fig. 11C); lateral margins of collar smooth, ventral lappets prominent, pointed and not overlapping (Fig. 11B,C). Ventral shields quadrangular, separated from the neuropodial tori, all similar in width (Fig. 11B). First ventral shield longer than the rest, with m-shaped

anterior margin although not conspicuous. First chaetiger with superior and inferior elongate narrowly hooded chaetae, superior longer than inferior (Fig. 11D). Rest of thoracic chaetigers with elongate narrowly hooded superior chaetae and broadly hooded inferior notochaetae with tips progressively tapering (type B) (Fig. 11E,G). Neuropodial tori slightly diminishing in width posteriorly. Thoracic uncini with several rows of small teeth, similar in size, above main fang (Fig. 11H); uncinus with well developed breast, handle twice length of the distance from breast to main fang (Fig. 4G). Companion chaetae with asymmetrical membrane and teeth covering about half the length (Fig. 11I). Neuropodia of anterior abdominal chaetigers with narrowly hooded chaetae (Fig. 11F). Notopodia with uncini similar to thoracic uncini (Fig. 11J) but with shorter handles (Fig. 4H). Pygidium trilobed from ventral view, as a rounded papilla from dorsal view, with scattered eyespots laterally. Tube made of a thin and flexible layer of mucus covered by a mixture of fine sediment and mud.

Variation. The paratypes range in size from 10–25 mm in length. The number of pairs of radioles varies from eight to ten. They possess one to two pairs of radiolar eyes (although the holotype possesses 3 pairs plus an extra eye on one side). One paratype (from AM W35505) also possesses dark, slightly inflated spots on the inner subdistal sides of most of the rest of the radioles (excluding the ventralmost three pairs) which could be incipient eyes. However, ommatidia could not be detected, and these therefore may just be pigmented areas.

Colour pattern. Pigment occurs at the base of radioles and in a few transverse irregular bands in radioles and pinnules. Body unpigmented.

Etymology. The name of this species is related to the conspicuously inflated peristomium. This feature is unique among other *Megalomma* species.

Remarks. This new species displays similar features to another species described in the Indo-Pacific area, *M. cinctum* from Taiwan—the fusion of dorsal collar margins to the faecal groove, the presence of dorsolateral pockets and the distribution of compound eyes in 1–3 dorsalmost pairs of radioles (this is if the spots found in one specimen are not considered as eyes). However *M. inflata* n.sp. is distinguished from *M. cinctum* by the conspicuous inflation of the peristomium shown in all the specimens, the deep U-shaped dorsolateral incisions of the collar (absent in *M. cinctum*), the presence of well-developed ventral sacs (absent in *M. cinctum*) and the narrowly hooded shape of the inferior thoracic chaetae (or at least slender and thin), but broadly hooded (type A) in *M. cinctum*.

There are species described from several localities around the world that share with this new species some features such as the development and shape of collar dorsal margins, collar margins fused to the faecal groove, the presence of pockets, eyes present on one to three dorsalmost pairs of radioles, and the absence of a caruncle. These are *M. coloratum* (Chamberlin, 1919) from California, *M. modestum* (de Quatre-fages, 1866) from Peru, *M. roulei* (Gravier, 1908) and *M. splendidum* (Moore, 1905). None of these species have an inflated peristomium, nor are their collar pockets as broad and U-shaped as *M. inflata* n.sp. Another species described from the Indian Ocean and which shares some features

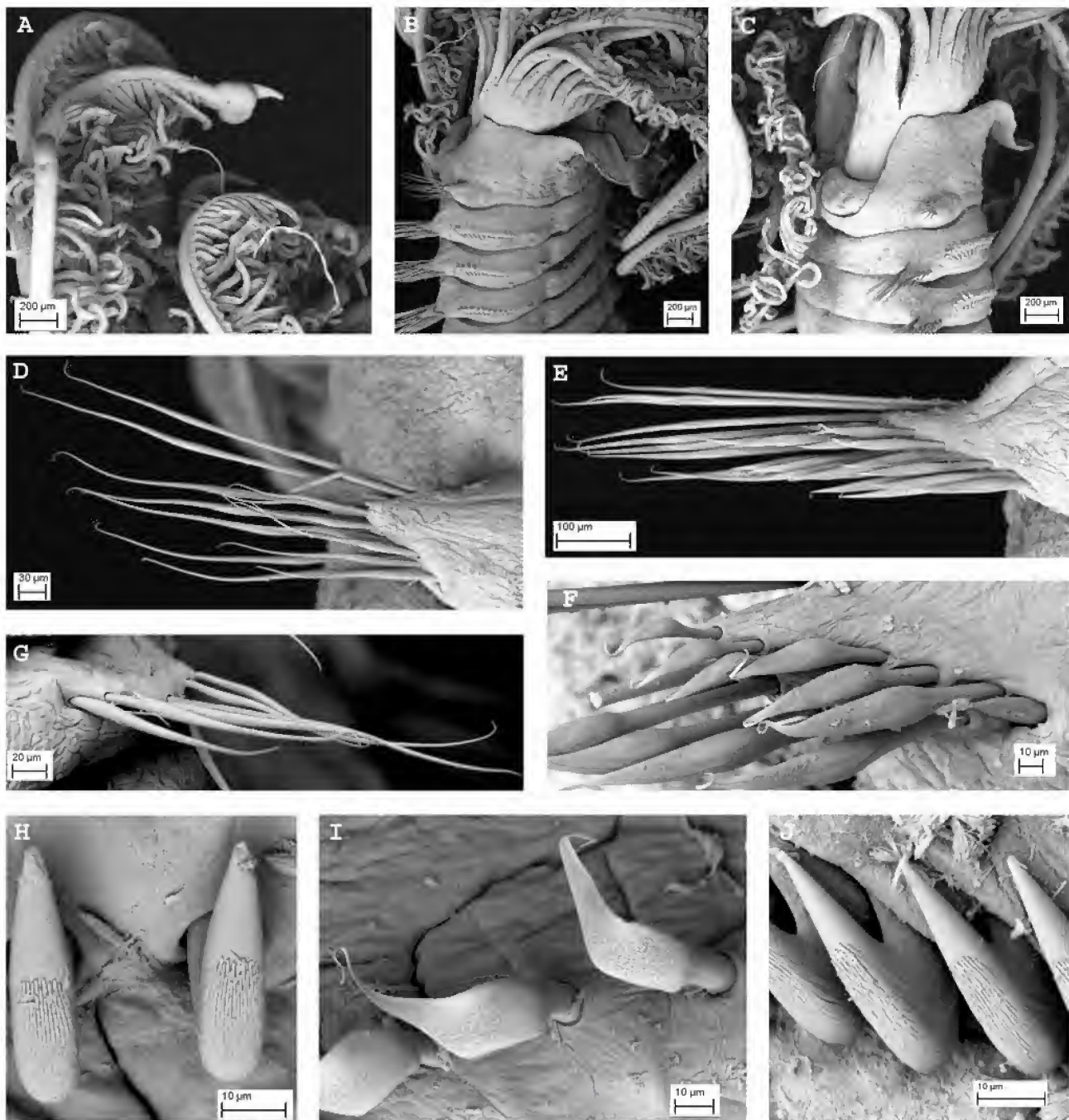


Figure 11. SEM of *Megalomma inflata* n.sp., AM W23057; (A) tip of radioles and dorsalmost compound subdistal eyes; (B) base of radiolar crown and anterior segments, lateral view; (C) margins of collar, dorsolateral view; (D) chaetae, first thoracic segment; (E) chaetae, anterior thoracic segment; (F) inferior thoracic chaetae, posterior thoracic segment; (G) abdominal chaetae; (H) thoracic uncini; (I) companion chaetae, same chaetiger; (J) anterior abdominal uncini.

with *M. inflata* n.sp. is *M. quadrioculatum* (Willey, 1905) but examination of the holotype for this review revealed the presence of a large caruncle, which is absent in the new species.

Megalomma sp. 1

Figs 2N–Q, 4I, J, 5E

Material examined. Queensland. AM W30022 (1 spec.), Abbott Point, near Bowen, 19°53'S 148°05'E, coll. by CRC Reef Research Centre Ltd for Queensland Ports Survey, from pylon scraping, 8 Jul. 1998, 7 m.

Description. Single specimen complete, measures 74 mm long (18 mm crown) and 5 mm wide. Crown longer than thorax, with 22 pairs of radioles in each lobe, arranged in a semicircle. External margin of radioles quadrangular at the base and rounded towards the tips (Fig. 2N,O,Q), without lateral flanges. Tips of radioles shorter than pinnules (Fig. 2Q). Radiolar skeleton with 15–20 cells in transverse section at the base of radioles (Fig. 5E). More than half (18–19) of the radioles with single subdistal compound eyes. Dorsalmost pair of radioles with large eye almost surrounding the tip of radiole, not spiral (Fig. 2Q); on adjacent radioles bearing subdistal eyes, eyes small and spherical, similar in size. Dorsal lips

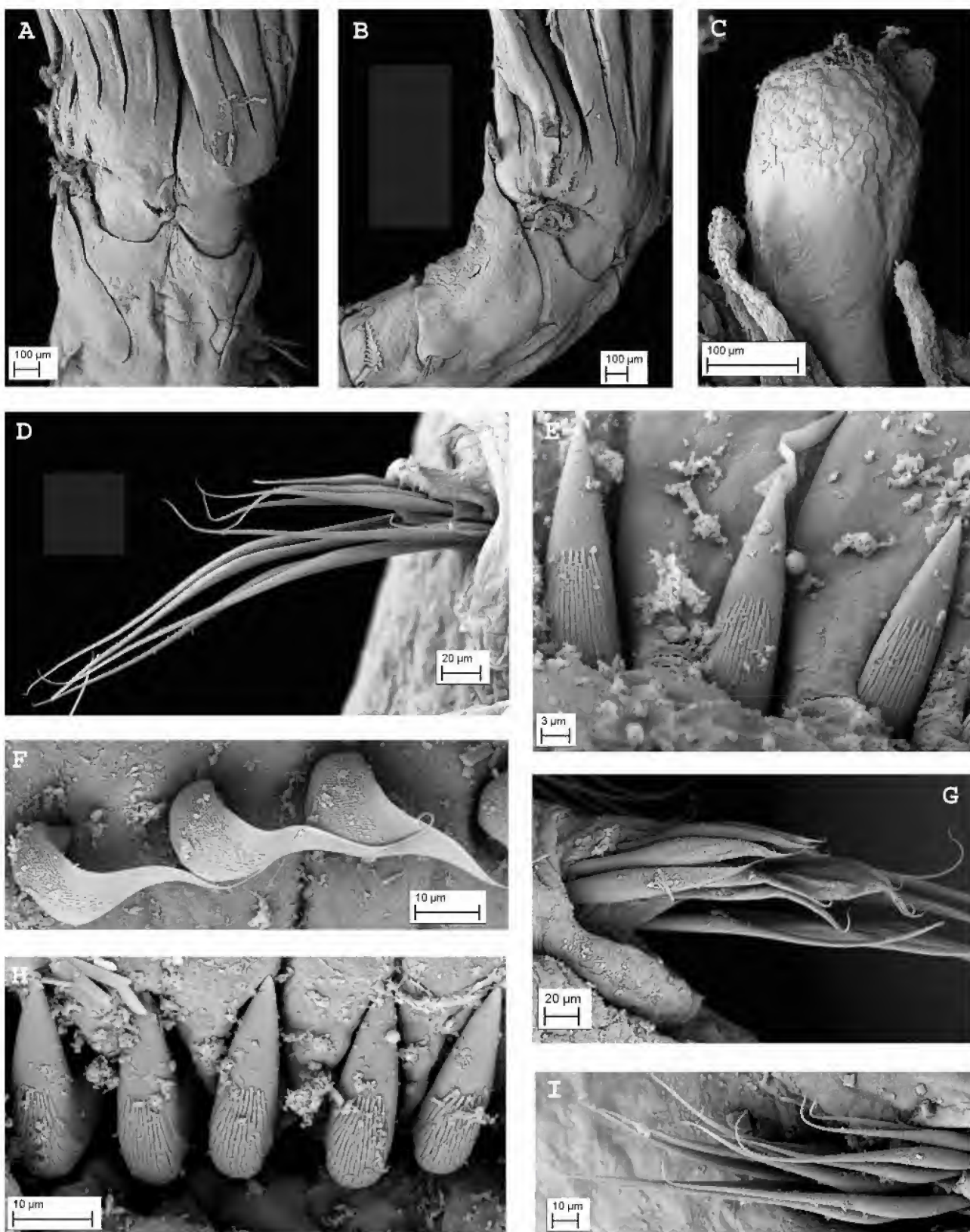


Figure 12. SEM of *Megalomma* sp. 2, MV F70842. (A) anterior thoracic chaetiger and posterior peristomial ring collar, dorsal view; (B) same, lateral view; (C) dorsal most subdistal radiolar eye; (D) notochaetae, first chaetiger; (E) uncini, anterior thoracic chaetiger; (F) companion chaetae, anterior thoracic chaetae; (G) posterior thoracic notochaetal fascicle, ventral view; (H) anterior abdominal uncini; (I) anterior abdominal neurochaetal fascicle.

with radiolar appendages as long as two thoracic chaetigers, lateral lamellae not reaching the tip of appendage, three dorsal pinnular appendages on each lip. Ventral lips rounded and well developed; parallel ventral lamellae and ventral sacs present. Caruncle absent. Smooth keel arising dorsally and directed ventrally between dorsal lips (Fig. 2O). Dorsal margins of collar fused to the faecal groove, with dorsolateral V-shaped notches on both sides and shallow dorsolateral pockets becoming a shallow groove more dorsally (Fig. 2O); lateral margins smooth (Fig. 2P), triangular non-overlapping ventral lappets, with a complete midventral incision (Fig. 2N). Ventral shields quadrangular with indented margins laterally, slightly diminishing in width posteriorly, in contact with the neuropodial tori, except in anterior chaetigers (Fig. 2N). First ventral shield 1.5 times longer than the rest, with an m-shaped anterior margin (Fig. 2N). First chaetiger with superior and inferior elongate narrowly hooded notochaetae, superior row longer than inferior. Rest of thoracic chaetigers with superior elongate narrowly hooded notochaetae arranged in irregular rows and inferior broadly hooded notochaetae (type B) in single row. Notopodia of thoracic chaetigers with a large lamellate lobe separating inferior and superior fascicles of notochaetae. Neuropodial tori becoming slightly shorter posteriorly. Thoracic uncini with several rows of small teeth, all similar in size above main fang; uncinus with well developed breast and handle about twice the length of the distance from breast to main fang (Fig. 4I). Companion chaetae with asymmetrical membrane. Abdominal neuropodia with broadly hooded chaetae. Notopodial uncini similar to thoracic uncini but with handles half their length (Fig. 4J). Posterior chaetigers regenerating, pygidium papilla-like, with scattered eyespots present.

Reproductive features. Eggs present in anterior abdominal segments.

Colour pattern. Crown and thorax with purple pigmentation after fixation. There are some conspicuous dark spots located on the ventral margin of the thoracic tori which we do not consider to be eyespots, as the patches are not discrete (pigment dilutes dorsally along tori edges) and they are also not interramal as in other sabellids that display segmental eyespots.

Remarks. This specimen does not fit the description of any previously described species but it is premature to describe it as new until more specimens are found and intraspecific variability can be assessed. The combination of such characters as margins of collar not fused to the faecal groove (although there is a ridge that continues from the end of the dorsal margins to where the middorsal faecal groove ends, which could be interpreted as fusion with the faecal groove), U-shaped dorsolateral incisions of the collar, the presence of low collar pockets, and subdistal eyes on most radioles makes the specimen similar to several other species previously described from the Indo-Pacific: *M. multioculatum*, from Thailand and *M. pacificum* from Gilbert Islands. However, *M. multioculatum* is described as having collar margins fused to the faecal groove and pockets present, and the latter species has been possibly referred to *Demonax* by Fitzhugh (2002). The specimen described above differs from *M. multioculatum* also in the development of the collar, as the ventral lappets are shorter, not visibly longer than lateral margins, but are elongate in *M. multioculatum*, in which the dorsal margins

of collar are clearly fused to the faecal groove and there are shallow pockets present on both sides. Also, the specimen from Queensland has inferior thoracic chaetae arising in a single row and with progressively tapering tips (type B) while *M. multioculatum* has chaetae with broader and more slender tips (type A). The handles of thoracic uncini are also shorter in the Queensland specimen.

According to Tovar-Hernández and Salazar-Vallejo (2008), there are three species described as having the dorsal margins of collar not fused to the faecal groove, pockets present and radiolar eyes in most radioles (which have been previously placed in Group 2B). One of these, *M. neapolitanum* Claparède, 1868, described from Italy, has been recently synonymized with *M. lanigera* (Grube, 1846) (Giangrande & Licciano, 2008). The other two, *M. heterops* and *M. perkinsi* Tovar-Hernández & Salazar-Vallejo, 2006, were described from Florida. The specimen described above differs from *M. heterops* in the shape of the inferior thoracic chaetae which are broader in the base and thinner in the tip, bottle-shaped, and the thoracic uncini handles which are significantly shorter. According to the drawings and original description, *M. perkinsi* has lateral and dorsal anterior margins of the collar similar in length, and the collar fused to the faecal groove, features not shared by the specimen described above.

Megalomma sp. 2

Fig. 12

Material examined. Victoria. MV F70842 (1spec. on SEM stub AM500), eastern Bass Strait, 8.6 km west southwest of Cape Conran, 37°51'11"S 148°38'32"E.

Description. Single specimen incomplete, with eight thoracic chaetigers and five abdominal chaetigers. Crown with ten pairs of radioles, arranged in semicircles. External margins of radioles quadrangular, without lateral flanges (Fig. 12A,B). Tips of radioles shorter than pinnules. Subdistal eyes present on the two dorsalmost pairs of radioles; dorsalmost pair larger and almost surrounding the radiolar tip (Fig. 12C). Ventral lips rounded and well developed; ventral parallel lamellae and ventral sacs present. Dorsal margins of collar not fused to the faecal groove, terminating dorsolaterally and leaving a wide gap between them (Fig. 12A,B); collar pockets absent; lateral margins smooth, oblique; elongate, triangular, non-overlapping ventral lappets, with a complete midventral incision. Ventral shields quadrangular, similar in length along thoracic chaetigers, almost in contact with tori. First ventral shield with a straight anterior margin. First chaetiger with superior and inferior elongate narrowly hooded notochaetae; superior row longer than the inferior (Fig. 12D). Rest of thoracic chaetigers with superior elongate narrowly hooded notochaetae and inferior broadly hooded notochaetae with tips decreasing in width progressively, arranged in two rows (Fig. 12G). Thoracic uncini with several rows of small teeth, all similar in size, above main fang (Fig. 12E), uncinus with well developed breast. Companion chaetae with asymmetrical membrane and small teeth covering most of surface but with smooth distal tip (Fig. 12F). Abdominal neuropodia with broadly hooded chaetae (Fig. 12I). Abdominal uncini similar to thoracic (Fig. 12H) but with shorter handles. Pygidium missing.

Remarks. *Megalomma* sp. 2 resembles most closely *M. cf. miyukiae* specimens described herein, in the development of the collar (with dorsal collar margins separated from the faecal groove), in the presence of radiolar eyes in the dorsalmost radioles, and in the absence of a caruncle, but these two species are distinguished by the shape of the collar margins, which end abruptly in *Megalomma* sp. 2, and form concave ends with low pockets in *M. cf. miyukiae*. Moreover ventral shields are separated from tori in this specimen, whereas these about in *M. cf. miyukiae*.

Results of cladistic analysis

Two trees of 39 steps were found after performing maximum parsimony analyses, with consistency and retention indices of 0.48 and 0.67 respectively. The first most parsimonious tree (Fig. 13) differs from the second in the position of *M. nechamae*, being in the second hypothesis the sistergroup of the clade *M. lanigera*–*M. suspiciens*.

In these two topologies the basal species include *M. kaikourense*, *M. gesae* Knight-Jones, 1997, *M. trioculatum*, *M. bioculatum* Ehlers, 1887, *M. interrupta* n.sp. and *M. cf. miyukiae*, considered by Knight Jones (1997) and subsequent authors as Group 2, although they do not form a monophyletic clade. These species all have dorsal margins not fused to faecal groove, which has been shown to be a

homoplastic character.

An apomorphic clade of *Megalomma* species, equivalent to Knight-Jones' Group 1, is supported by two synapomorphies, collar margins fused to the faecal groove (character 6) and the presence of pockets (character 7). Two clades are also nested within this; one is supported by the presence of dorsal collar lappets (character 8) and the other by the presence of narrowly hooded abdominal chaetae (character 14), the latter being homoplastic and of dubious worth as it should be checked in several species. The jackknife support values are lower than 37 in all the clades except for the clade *Megalomma* supported by a 100 jk value, suggesting that more evidence for confirming these results is needed.

The new species are not closely related and belong to different clades, denoting that there is not a common ancestor for the Australian species. *Megalomma interrupta* n.sp. is one of the basal species due to the plesiomorphic condition of collar margins not fused to the faecal groove, while *M. phyllisae* n.sp. and *M. inflata* n.sp. belong to the apomorphic *Megalomma* clade with dorsal collar margins fused to the faecal groove and presence of collar pockets. The two latter species belong to different groups, *M. phyllisae* n.sp. being nested with those species with dorsal collar lappets, and *M. inflata* n.sp. with those species with narrowly hooded abdominal chaetae.

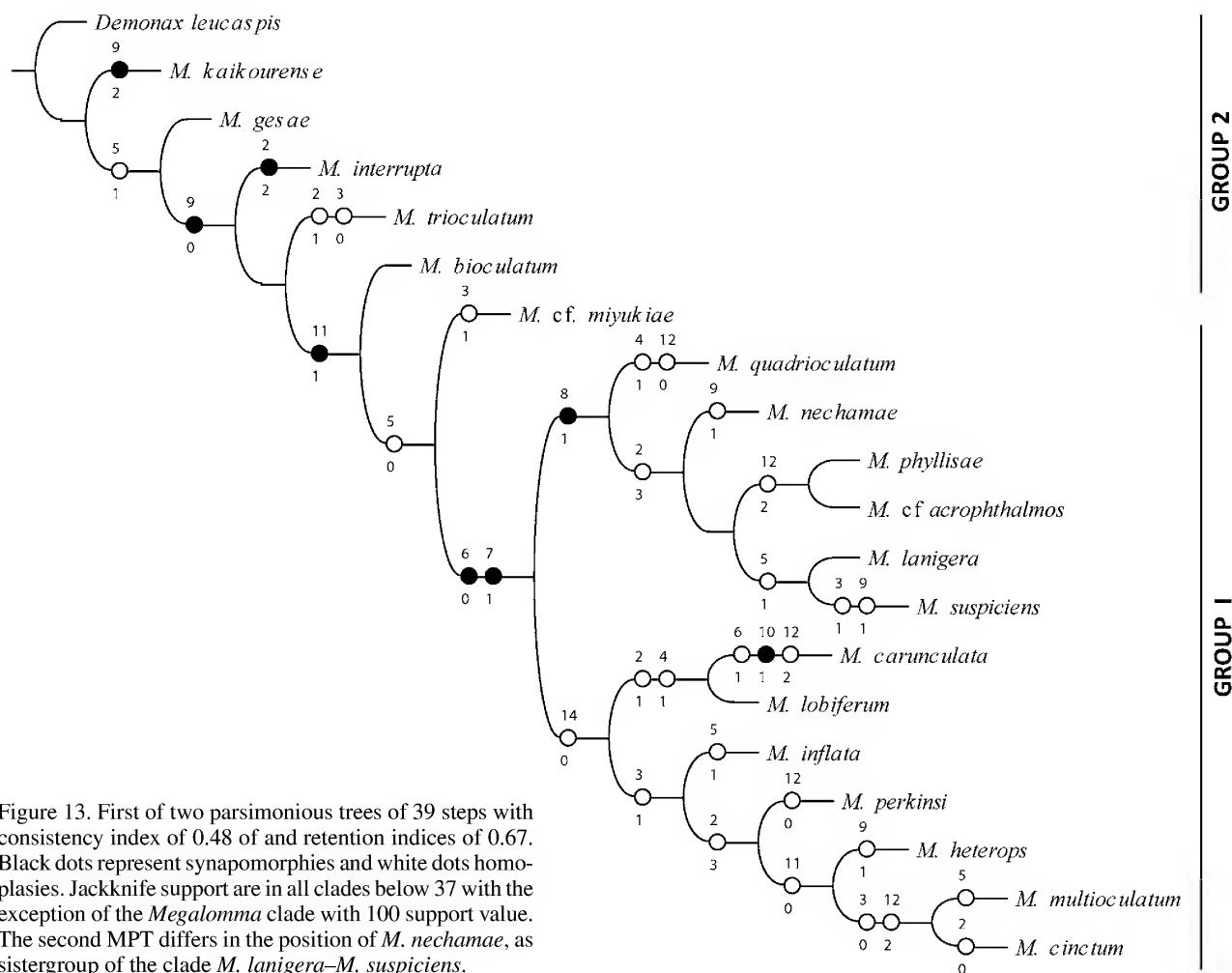


Figure 13. First of two parsimonious trees of 39 steps with consistency index of 0.48 and retention indices of 0.67. Black dots represent synapomorphies and white dots homoplasies. Jackknife support are in all clades below 37 with the exception of the *Megalomma* clade with 100 support value. The second MPT differs in the position of *M. nechamae*, as sistergroup of the clade *M. lanigera*–*M. suspiciens*.

Table 2. Summary of groups proposed by Knight-Jones (1997) and subsequent authors, including combinations of characters not considered previously. Some taxa have been moved to different groups after examination of type material or re-interpretation of original descriptions and drawings. NSW: New South Wales, NT: Northern Territory, QLD: Queensland, VIC: Victoria, WA: Western Australia.

group	dorsal collar margins	pockets	subdistal radiolar eyes	caruncle	number species before this study	species from Australia
1A	fused to faecal groove	present	most	absent	<i>M. acrophthalmos</i> <i>M. circumspectum</i> <i>M. claparedii</i> <i>M. fauchaldi</i> <i>M. heterops</i> ^a <i>M. lanigera</i> ^b <i>M. multioculatum</i> <i>M. pacifici</i> <i>M. pacificum</i> <i>M. perkinsi</i> ^c <i>M. suspiciens</i> ^d <i>M. vesiculosum</i> <i>?M. vigilans</i>	<i>M. phyllisae</i> (VIC) <i>M. cf. acrophthalmo</i> (WA) <i>Megalomma</i> sp. 1 (QLD)
				present	<i>M. carunculata</i> <i>M. "de l'étang de Thau"</i> <i>M. lobiferum</i>	
1B			1–3 dorsalmost	absent	<i>M. cinctum</i> <i>M. coloratum</i> <i>M. mechamae</i> ^e <i>M. modestum</i> <i>M. mushaenese</i> ^f <i>M. roulei</i> <i>M. splendidum</i>	<i>M. inflata</i> (NSW)
1C			dorsalmost and lateral	present	<i>M. quadrioculatum</i>	
2A	not fused to faecal groove	present	most	absent	<i>(M. neapolitanicum)</i> ^g	
2A2			dorsalmost	absent	<i>M. kaikourense</i> ^h	
2B		absent	one dorsalmost	absent	<i>M. bioculatum</i> <i>M. gesae</i>	
				present	<i>M. pigmentum</i>	
2C		most	absent	<i>M. trioculatum</i> ⁱ	<i>Megalomma</i> sp. 2 (VIC)	
2D	1–5 dorsalmost	absent	<i>M. miyukiae</i>	<i>M. cf. miyukiae</i> (NT, QLD)		
2E		present	dorsalmost and lateral	absent		<i>M. interrupta</i> (QLD, WA, Indonesia)

a Dorsal collar margins in *Megalomma heterops* have been interpreted herein as fused to faecal groove (Tovar-Hernández & Salazar-Vallejo, 2006).
 b *Megalomma lanigera* is considered a valid species by Giangrande & Licciano (2008).
 c Dorsal collar margins in *Megalomma perkinsi* have been interpreted herein as fused to faecal groove (Tovar-Hernández & Salazar-Vallejo, 2006).
 d After examination of type material we confirm that *M. suspiciens* does not possess a caruncle.
 e *Megalomma* "de l'étang de Thau" was recorded from southern France by Brunotte (1888), as *Branchiomma* and is considered a valid *Megalomma* species (Tovar-Hernández & Salazar-Vallejo, 2008).
 f *Megalomma mushaense* and *M. nechamae* were allocated to Group 2C (Knight-Jones, 1997) and were described as possessing dorsal lappets, but as this feature is not possible without interpreting the dorsal collar margins as fused to faecal groove, these species should be moved to Group 1B.
 g *Megalomma neapolitanum* is now considered a junior synonym of *M. lanigera* (Giangrande & Licciano, 2008), leaving only two species in Group 2B.
 h *Megalomma kaikourense* was described as possessing vestigial pockets (Knight-Jones, 1997).
 i After examination of paratypes, we find that the dorsal collar margins are not fused to faecal groove and pockets are absent.

Key to Australian species of *Megalomma*

- 1 Dorsal collar margins fused to the faecal groove 2
- Dorsal collar margins well separated 4
- 2 Dorsal collar lappets present 3
- Dorsal lappets absent *M. inflata* n.sp.
- 3 Lappets large, spatulate in shape *M. cf. acrophthalmos*
- Low lappets. Over 20 rows cells in radiolar skeleton *M. phyllisae* n.sp.
- 4 Subdistal eyes in dorsalmost and lateral radioles *M. interrupta* n.sp.
- Subdistal eyes present only in dorsal most radioles (1–3 pairs) *M. cf. miyukiae*

Table 3. Matrix of fourteen morphological characters and a variety of species of *Megalomma* from all the categories proposed by Knight-Jones (1997) together with the species described in Australia.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>Demonax leucaspis</i>	0	—	2	0	0	1	0	0	1	0	0	1	0	0
<i>Megalomma lanigera</i>	1	3	2	0	1	0	1	1	0	0	1	1	1	1
<i>M. multioculatum</i>	1	3	0	0	1	0	1	0	0	0	0	2	1	0
<i>M. carunculata</i>	1	1	2	1	0	1	1	0	0	1	1	2	1	0
<i>M. cinctum</i>	1	0	0	0	0	0	1	0	0	0	0	2	1	0
<i>M. heterops</i>	1	3	1	0	0	0	1	0	1	0	0	1	1	0
<i>M. perkinsi</i>	1	3	?	0	0	0	1	0	0	0	1	0	1	?
<i>M. gesae</i>	1	0	?	0	1	1	0	0	1	0	0	?	1	?
<i>M. kaikourense</i>	1	0	?	0	0	1	0	0	2	0	0	1	1	1
<i>M. nechamae</i>	1	3	?	0	0	0	1	1	1	0	1	1	1	1
<i>M. cf. miyukiae</i>	1	0	1	0	0	1	0	0	0	0	1	1	1	1
<i>M. phyllisae</i>	1	3	2	0	0	0	1	1	0	0	1	2	1	1
<i>M. interrupta</i>	1	2	2	0	1	1	0	0	0	0	0	1	1	1
<i>M. lobiferum</i>	1	1	?	1	0	0	1	0	0	0	1	1	1	?
<i>M. suspiciens</i>	1	3	1	0	1	0	1	1	1	0	1	1	1	1
<i>M. cf. acrophthalmos</i>	1	3	2	0	0	0	1	1	0	0	1	2	1	1
<i>M. trioculatum</i>	1	1	0	0	1	1	0	0	0	0	0	1	1	1
<i>M. bioculatum</i>	1	0	?	0	1	1	0	0	0	0	1	1	1	?
<i>M. inflata</i>	1	0	1	0	1	0	1	0	0	0	1	1	1	0
<i>M. quadrioculatum</i>	1	0	2	1	0	0	1	1	0	0	1	0	1	1

Discussion

Although *Megalomma* has been considered a cosmopolitan genus (see Knight-Jones, 1997) it is not very abundant in benthic habitats and this is reflected in the number of specimens collected and recorded in ecological and taxonomic studies. For instance, several authors have described new species based on scarce material: Fitzhugh's (2002) description of *M. multioculatum* is based on a single specimen, *M. carunculata* is described from three specimens (Tovar-Hernández & Salazar-Vallejo, 2008), *M. miyukiae*, also described from three specimens (Nishi, 1998), *M. perkinsi* from two (Tovar-Hernández & Salazar-Vallejo, 2006), *M. nechamae* from seven, *M. kaikourense* from six, *M. messapicum* from 12, and *M. gesae* from ten (Knight-Jones, 1997). Similar results have been observed after the study of a vast collection of sabellids from several surveys around Australia from which only 62 specimens of *Megalomma* have been found. This justifies the description of three new species even though there was insufficient material to document intraspecific variation in some cases.

Results from the present study show that the genus is well-represented along Australian coasts, living in several habitats and depths, and that diversity is greater than previously thought, as there are at least seven species, three of them new.

Results of cladistic analysis reveal that some of the features selected by Knight-Jones (1997) to establish groups of species are valid and gather natural groups, and

these are the fusion of dorsal collar margins and presence of collar pockets. Results also illustrate that the presence of dorsal lappets and shape of abdominal chaetae are useful characters for grouping species. The fusion of dorsal collar margins to the faecal groove and the presence of pockets characterizes an apomorphic clade of *Megalomma* species, in which a clade with dorsal lappets is nested. Nevertheless, the number and distribution of radiolar eyes are homoplastic characters varying substantially in the *Megalomma* radiation and therefore are not suitable for classification.

Conclusions

After examination of specimens collected during many surveys around the Australian coast and housed in the three main Australian museum collections (AM, MV and MAGNT), we have documented the presence of the genus *Megalomma* in this continent, and have found it to exhibit high diversity, albeit in low numbers. These findings are similar to previous studies in other geographic areas.

The total number of *Megalomma* species before the present study was 31 and is now increased to 34.

We found in this study that intraspecific morphological variation may be high and affects several features previously considered as diagnostic.

A worldwide revision of the genus is needed in order to clarify some issues partially commented on in this study.

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